

WHITE PAPER

**Predation on Salmonids
Relative to the Federal Columbia River Power System**

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FORWARD

The purpose of this white paper is to provide a synthesis of scientific information regarding predation on anadromous salmonids as it relates to the existence and current operation of the hydropower system. Other white papers are available that address the effects of river flow and dam passage on salmonids. A fourth white paper provides a synthesis of scientific information on the effects of transporting juvenile salmonids around dams to mitigate for losses of juvenile migrants that would otherwise migrate downstream through the dams on the lower Snake and Columbia rivers. These papers are available on the Northwest Fisheries Science Center home page (www.nwfsc.noaa.gov/pubs/nwfscpubs.html).

The white papers do not address the possible effects on salmonids that might accrue from major changes to the present configuration of the hydropower system (e.g., draw down or dam removal); nor do they speculate about potential indirect effects (e.g., delayed mortality) that might occur as a result of hydropower system passage. Empirical data on these subjects are scarce. Other forums, such as the Plan for Analyzing and Testing Hypotheses (PATH) and the Cumulative Risk Initiative (CRI), are addressing these issues. Nonetheless, it is recognized that many of the impacts of dams on migrant fish, as identified in the white papers, would decrease with removal of dams. Most analyses conducted to date indicate that removal of dams would lead to higher direct survival of migrant fish. Such findings are not inconsistent with anything presented in this white paper.

Following regional review beginning in October 1999, this white paper has been modified to reflect comments and information provided by numerous reviewers and resource agencies including Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, Columbia Basin Fish and Wildlife Authority, Washington Department of Fish and Wildlife, Columbia River Inter-Tribal Fish Commission, U.S. Geological Survey, and Fish Passage Center.

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INTRODUCTION

The Columbia and Snake Rivers formerly supported a great abundance of anadromous salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*). Chapman (1986) conservatively estimated that the number of adult salmonids returning to the Columbia Basin has declined during this century from approximately 7.5 million to less than 2.5 million annually. Initially, human predation (i.e., unrestricted harvest) was the major factor in the decline of these anadromous salmonid runs, but this was followed by widespread impacts to upriver spawning runs that resulted from the construction and operation of hydroelectric dams. In addition to juvenile and adult passage problems associated with dams throughout the Federal Columbia River Power System (FCRPS), much of the freshwater ecosystem upon which Columbia and Snake River anadromous salmonids depend was transformed from a free-flowing riverine system into a series of reservoirs. Given the perturbed state of this ecosystem, salmonid predation by resident fish, birds, and marine mammals – once in relative balance with healthy salmonid populations – now contributes significantly to higher levels of cumulative life-cycle mortality.

This report is a synthesis of information regarding predation on anadromous salmonids as it relates to the existence and current operation of the FCRPS. The focus is on existing conditions, in the context of known or likely effects of the FCRPS on predator populations and predator-prey interactions.

Dams and reservoirs are generally believed to have increased the incidence of predation over historic levels (Poe et al. 1994). Brown and Moyle (1981) reviewed the literature on northern pikeminnow predation and concluded that lentic habitats and disruption of habitat or prey behavior may exacerbate the effects of northern pikeminnow predation. Impoundments in the Columbia River Basin increase availability of microhabitats within the range preferred by northern pikeminnow and other predators (Faler et al. 1988, Beamesderfer 1992, Mesa and Olson 1993, Poe et al. 1994), may increase local water temperatures which increases digestion and consumption rates by northern pikeminnow (Falter 1969, Steigenberger and Larkin 1974, Beyer et al. 1988, Vigg and Burley 1991, Vigg et al. 1991), decrease turbidity which may increase capture efficiency of predators (Gray and Rondorf 1986), favor introduced competitors which could cause some predators to shift to a diet composed largely of juvenile salmonids (Poe et al. 1994), and increase stress and subclinical disease of juvenile salmonids which could increase susceptibility to predation (Rieman et al. 1991, Gadomski et al. 1994, Mesa 1994). In addition, dam-related passage problems and reduced river discharge can affect the availability, distribution, timing, and aggregation of migrating salmonids, thereby increasing exposure time to predation (Raymond 1968, 1969, 1979, 1988; Park 1969, Van Hynning 1973, Bentley and Raymond 1976) and, in particular, increasing exposure time later in the season when predator consumption rates are high (Beamesderfer et al. 1990, Rieman et al. 1991).

In the sections on piscine, avian, and marine mammal predator populations to follow, information (where available) is presented regarding the following elements:

- Brief description of the biology of predator species.
- Description of the effects of the FCRPS on this predator species population.
(e. g., water temperature, prey and predator densities).

- Description of predation on juvenile salmon (e. g., diet composition, salmonid consumption rates, population size, and estimated total impact of the predator population).
- Effects of predator management (including removal) on predator and prey populations and the effects of other, non-lethal, predator control measures (e.g., outfall siting, spill patterns, avian lines, harassment).
- Critical scientific uncertainties.

PISCINE PREDATOR POPULATIONS

The Columbia River Basin has a diverse assemblage of native and introduced fish species. A list of piscivore and prey fish species found in the anadromous portion of the Columbia Basin is presented in Table 1 (Ward 1997).

Table 1. Resident piscivores (based on adult diets) and potential prey species of the mainstem lower Columbia River Basin.

Trophic classification	Common name	Scientific name
Piscivore:	Northern pikeminnow (Northern squawfish)	<i>Ptychocheilus oregonensis</i>
	Channel catfish	<i>Ictalurus punctatus</i>
	Smallmouth bass	<i>Micropterus dolomieu</i>
	Walleye	<i>Stizostedion vitreum</i>
Potential prey:	Pacific lamprey	<i>Lampetra tridentata</i>
	American shad	<i>Alosa sapidissima</i>
	Chinook salmon	<i>Oncorhynchus tshawytscha</i>
	Steelhead	<i>O. mykiss</i>
	Mountain whitefish	<i>Prosopium williamsoni</i>
	Bullhead	<i>Amerius</i> spp.
	Peamouth	<i>Mylocheilus caurinus</i>
	Chiselmouth	<i>Acrocheilus alutaceus</i>
	Common carp	<i>Cyprinus carpio</i>
	Redside shiner	<i>Richardsonius balteatus</i>
	Longnose dace	<i>Rhinichthys cataractae</i>
	Largescale sucker	<i>Catostomus macrocheilus</i>
	Bridgelip sucker	<i>Catostomus columbianus</i>
	Threespine stickleback	<i>Gasterosteus aculeatus</i>
	Sand roller	<i>Percopsis transmontana</i>
	Bluegill	<i>Lepomis macrochirus</i>
	Pumpkinseed	<i>L. gibbosus</i>
	Crappie	<i>Pomoxis</i> spp.
	Yellow perch	<i>Perca flavescens</i>
	Prickly sculpin	<i>Cottus asper</i>

Northern Pikeminnow

The genus *Ptychocheilus*, represented by four contemporary species, had widespread distribution in the Pliocene epoch -- and may be considered a generalist in life history patterns since it adapted successfully to both lacustrine and riverine systems (Smith 1975, Tyus 1986). The native northern pikeminnow (*Ptychocheilus oregonensis*) is the dominant piscine predator of juvenile salmonids in the Columbia River system, and predation by this species is clearly important in relation to other sources of mortality (Poe et al. 1991, Rieman et al. 1991, Vigg et al. 1991, Ward and Zimmerman in press, Zimmerman in press). Northern pikeminnow were commonly known as northern squawfish until 1998 (Nelson et al. 1998).

Biological Attributes of Northern Pikeminnow Relative to Predation on Juvenile Salmonids

Northern pikeminnow are large, long-lived, slow-growing, predaceous cyprinids whose unexploited populations are typically dominated by large, old individuals (Beamesderfer et al. 1996). Maximum fork length, weight, and age are approximately 600 mm, 2.5 kg, and 16 years in the Columbia River (Rieman and Beamesderfer 1990, Parker et al. 1995). Annual mortality rates are 12-31% (Rieman and Beamesderfer 1990, Parker et al. 1995).

In terms of spawning behavior and habitat preference, Balon (1975) categorized northern pikeminnow within the ecoethological guild of nonguarders, open substrate spawners, and lithophils. Much of the information on northern pikeminnow spawning behavior and habitat requirements is documented in unpublished theses (e.g., Teraguchi 1962, Casey 1962, Howse 1966, Reid 1971, Olney 1975, Beamesderfer 1983). Patten and Rodman (1969) observed northern pikeminnow spawning in a reservoir on a tributary stream of the lower Columbia River; peak spawning occurred in the first week of July on steep rocky shores at depths of 3 to 15 m (epilimnion) and temperatures of about 17° C. Lake-dwelling populations are also known to migrate into streams to spawn, especially when a gravel shore is not available in the lake (Jeppson and Platts 1959). A review of the literature on reproductive characteristics of northern pikeminnow in various habitats is presented in Table 2.

Table 2. Reproductive characteristics of northern pikeminnow in various waters (Vigg et al. 1990).

CHARACTERISTIC	HABITAT	REFERENCE
Sex Ratio:		
1.8:1 to 5.5:1 (females: male)	John Day Reservoir and tailrace, WA & OR	Vigg et al. (1990)
50:1 to 200:1 (males:females)	Merwin Reservoir, WA	Patten and Rodman (1969)
Spawning Time:		
mid June-August	John Day Reservoir and tailrace, WA & OR	Vigg et al. (1990)
April-early June	Cultis Lake, BC	Foerster and Ricker (1941)
May-June	Sixteenmile Lake tributaries, BC	Teraguchi (1962)
June	Cooper & Seeley Lakes, MT	Hill (1962)
June	Anderson Ranch Reservoir, ID	Pollard (1971)
June	Cascade Reservoir tributaries, ID	Casey (1962)
June-July	Payette Lake tributaries, ID	Casey (1962)
Mid June-mid July	Hayden Lake, ID	Jeppson (1957)
Mid June-mid July	St. Joe River, ID	Reid (1971)
Late June-mid or late July	St. Joe River, ID	Beamesderfer (1983)
Late June-early July	Merwin Reservoir, WA	Patten and Rodman (1969)
early June-early August	Lake Washington, WA	Olney (1975)
May-early Sept.	John Day Reservoir and tailrace, WA & OR	Henchman (1986)
Spawning Temperature(°C):		
13-21	John Day Reservoir and tailrace, WA & OR	Vigg et al. (1990)
12-20	Cooper & Seeley Lakes, MT	Hill (1962)
10-20	Cascade Reservoir tributaries, ID	Casey (1962)
10	Payette Lake tributaries, ID	Casey (1962)
14-20	Hayden Lake, ID	Jeppson (1957)
10-20	St. Joe River, ID	Reid (1971)
11-18	St. Joe River, ID	Beamesderfer (1983)
17	Merwin Reservoir, WA	Patten and Rodman (1969)
13.5-20	Lake Washington, WA	Olney (1975)
Fecundity (fish size):		
16,357-35,820	Columbia Basin	Knutsen and Ward (1997)
37,000-83,000 (407-521 mm, n=4)	Hayden Lake, ID	Jeppson (1957)
mean= 20,136 eggs (mean	St. Joe River, ID	Reid (1971)

FL= 391 mm)

2,700-75,115 eggs (260-566 mm FL) Lake Washington, WA

Olney (1975)

6,037-95,089 eggs (342-590 TL; 396-1956 g)

Eggs= $45.5 \cdot (\text{Wgt}) - 4532$
(n=41, r= 0.877)

Gonadal Somatic Index:

Females: 7 Males: 2.8
(max. monthly mean)

John Day Reservoir and
tailrace, WA & OR

Vigg et al. (1990)

Females: 5-16

St. Joe River, ID

Beamesderfer (1983)

Males: 0.5-7

Females: 9.9

Lake Washington, WA

Olney (1975)

Males: 4.6

(max. monthly mean)

Length at Sexual Maturity:

Females: > 310

Cascade Reservoir, ID

Casey (1962)

Males : > 250

Males: > 250

Round Lake, ID

Howse (1966)

Females: 286-336

St. Joe River, ID

Reid (1971)

Males: 261-297

Females: 265-380

St. Joe River, ID

Beamesderfer (1983)

(most > 300)

Males: 230-285

(most > 250)

Females: 301-350

Lake Washington, WA

Olney (1975)

Males: 251-275

Age at Sexual Maturity:

Females: 7-9

Alva Lake, MT

Hill (1962)

Males: 6

Females: 4

Cascade Reservoir, ID

Casey (1962)

Males: 4-5 (most at 5)

Males: 5

Round Lake, ID

Howse (1966)

Females: 6-7

St. Joe River, ID

Reid (1971)

Males: 5-6

Females: 5-9 (most at 7)

St. Joe River, ID

Beamesderfer (1983)

Males: 5-8 (most at 6)

Females: 4-7 (most at 6)

Lake Washington, WA

Olney (1975)

Males: 4-6 (most at 5)

Spawning Habitat &

Substrate:

Riffle areas over rubble or
rock

Cascade Reservoir, ID

Casey (1962)

Shoal areas over rubble

Hayden Lake, ID

Jeppson (1957)

Tributary streams

Lakes, ID

Jeppson and Platts (1959)

Pools (shallow tail end) and
slow glides over rubble and

St. Joe River, ID

Reid (1971)

boulders (spawn not observed)

Gravel & cobble (1-30 cm), depth 1.3-9.5 m, bottom velocity low (0.2-1.4 fps), nearby slack water for adult congregation. Two substrate types: (1) Surface velocity > bottom velocity -- depth is shallow; (2) Surface & bottom similar velocity -- deep water.

St. Joe River, ID

Beamesderfer (1983)

Steep shore, talus slope (30°), 3-15 m depth.

Merwin Reservoir, WA

Patten and Rodman (1969)

Spawning Behavior

The spawning population of northern pikeminnow in Merwin Reservoir, Washington consisted of up to 8,000 fish having an estimated sex ratio of 50 to 200 males per female (Patten and Rodman 1969). "Swarming" behavior was observed, with one to six males chasing a female -- culminating in a spawning act of less than one second duration when pale, demersal, 1-mm diameter eggs were broadcast about 3 cm off the bottom, some eggs being deposited in rock interstices. The effects of dams on reproductive ecology is not well understood (e.g., are northern pikeminnow fertilized eggs and larvae distributed downstream due to flow patterns or are spawning areas also utilized as nursery areas?). As a comparison, the spawning of Colorado pikeminnow (*P. lucius*), a potamodromous riverine species, occurs in middle to late summer under a decreasing flow regimen -- conditions postulated to distribute young downstream into shallow nursery habitat (Tyus 1986).

Spawning Timing, Gonadal Development, and Fecundity

Spawning generally occurs in June and July in large aggregations which broadcast eggs over clean rocky substrate in slow-moving water at a wide range of depths in rivers, lake tributaries, lake outlet streams, and shallow and deep littoral areas (Beamesderfer 1992). Based on the pattern of mean gonadal somatic index (1982 and 1986), and the stage of maturity index (1982-1986), Vigg et al. (1990) infer that the peak spawning period for northern pikeminnow in John Day Reservoir and tailrace occurs from about 9 June to 15 July¹. The mean GSI of northern pikeminnow in 1982 and 1986 peaked in June for both sexes. In 1982, female GSI increased from 4.4 in May to a peak of 6.6 on 2 June, with a subsequent decline to 1.6 by the end of July. Males had a similar pattern, but the time

¹The Gonadal Somatic Index (GSI) is the weight of the fishes' gonads, expressed as a percentage of body weight; i.e., cg gonad *g fish⁻¹. A subjective maturity index of 0 to 4 (Nikolsky 1963, Snyder 1983) was assigned in the field using visual examination of the dissected gonads.

frame was shorter; mean GSI increased from 1.3 in May to a peak of 3.0 by 15 June 1982 and declined to 0.4 during the first week in July. After August, when spawning was over, female GSI ranged from 1.1 to 2.9, and male GSI ranged from 0.4 to 1.2. The GSI pattern in 1986 was very similar to that observed in 1982. During 1986, female GSI increased to 14.4 by 9 June and declined to 2.7 by August. Male GSI also peaked at 4.5 by 9 June and decreased to 0.6 in August.

The changes in mean GSI for both sexes were statistically different by month. In 1982, GSIs for females and males were significantly different in May and June compared to July and August ($P < 0.05$). In 1986, May and June GSI values were significantly different from those in April, July, and August ($P < 0.05$). For both sexes, the mean weight and condition factor significantly decreased in July and August (i.e., during and after spawning) (Table 3). Mean weight of females in July and August was about 13.6% less than during April-June -- this is

Table 3. Mean size characteristics of female and male northern pikeminnow sampled from John Day Reservoir during April-August 1982-1986 (Vigg et al. 1990).

Sex	Month	Sample Size (n)	F: 1 M	Weight (g)	Fork Length (mm)	Condition Factor (K^1)
Female:	April	444	4.7	1069	424	1.36
	May	820	3.8	1055	416	1.41
	June	982	5.5	1016	417	1.35
	July	536	1.8	951	422	1.23
	August	750	2.6	857	407	1.22
Male:	April	95		575	354	1.24
	May	218		509	337	1.29
	June	177		500	336	1.27
	July	295		420	325	1.14
	August	284		448	334	1.26

$K^1 = \text{Weight } 10^5 / \text{Length}^3$.

about the same percentage as GSI, and is probably due to gonad weight loss. Mean weight loss of males (17.8%) during July and August was considerably higher than the percent gonad weight, and may indicate a protracted period of gamete loss (energy loss) or depression of feeding activity.

Sexual maturity occurs at sizes of 200 to 350 mm and ages of 3 to 8 years with males typically maturing sooner than females (Beamesderfer 1992, Parker et al. 1995). The maturity index during 1982-1986 was consistent with the GSI pattern (Vigg et al. 1990). For males and females, over 79% of the northern pikeminnow population was sexually developing during the months of April and May. In June, this trend reversed as the proportion of "developing" northern pikeminnow decreased as they became "ripe." From June to August, the proportion of "spent" northern pikeminnow increased from 8 to 61% for females and 2 to 39% for males.

Individual fecundity of northern pikeminnow averages about 25,000 eggs per female (Parker et al. 1995). Knutsen and Ward (1997) present fecundity of various populations of northern pikeminnow throughout the Columbia Basin (Table 4).

Table 4. Mean fecundity and mean (SD) relative fecundity (number of eggs per gram body weight) of female northern pikeminnow. Fecundities (with weight as covariate) for each area without a letter in common were significantly different ($P < 0.01$). Analyses limited to areas and years with $n \geq 10$ (Knutsen and Ward 1997).

Area, Year	n	Fecundity	Relative Fecundity
Downstream from Bonneville Dam			
1991	74	36,359 z	38.5 (15.9)
1992	294	25,036 zy	37.1 (15.0)
1993	295	22,465 y	36.2 (27.0)
1994	93	26,616 zy	35.8 (10.8)
1995	151	18,497 x	28.9 (12.1)
1996	50	24,567 zy	39.3 (8.6)
Bonneville Reservoir			
1991	46	35,820 z	43.5 (47.1)
1992	113	33,429 z	34.6 (11.4)
1993	106	29,846 zx	31.2 (11.4)
1994	116	28,347 yx	31.1 (12.2)
1995	6	18,550 --	22.3 (8.0)
1996	57	25,550 zy	31.6 (8.2)
John Day Reservoir			
1991	82	30,422 zy	28.1 (10.0)
1992	119	31,504 z	31.6 (8.8)
1993	108	25,340 x	23.7 (8.3)
1994	64	27,321 yx	24.5 (8.2)
1995	16	16,357 w	18.3 (6.7)
1996	66	35,044 z	29.7 (8.3)
Lower Granite Reservoir			
1991	51	26,594 z	31.6 (11.5)
1992	35	25,393 z	26.6 (11.0)
1993	20	30,422 z	26.1 (10.2)
1994	5	21,926 --	34.3 (22.9)
1995	8	24,053 --	20.1 (10.0)
1996	81	26,816 z	28.4 (9.1)

Sex Ratio

The ratio of females to males throughout the reservoir peaked in June, followed by a sharp decline in July. The ratio of females to males was consistently higher in the McNary Dam tailrace than in the main reservoir, but the temporal trend was similar. During all months (April to August), females were significantly longer, heavier, and had a higher condition factor than males (ANOVA, $P < 0.05$; Table 3).

Spawning Effects on Feeding

Corresponding to the presence of "spent" northern pikeminnow in June, the percentage of empty stomachs also increased. Vigg et al. (1990) hypothesized that the increased incidence of empty stomachs is partly due to a depression of feeding activity related to spawning. The observed increase in empty stomachs is probably also due, in part, to increased digestion rate caused by increasing temperatures. In the John Day pool, the proportion of empty stomachs increased from 27% in May to 41% in June; likewise, in the McNary tailrace boat-restricted zone the percent empty stomachs increased from 18 to 32%. In both areas, the percent of empty stomachs subsequently declined in July and increased again to about 35% in the John Day pool and over 50% in the McNary Dam tailrace.

Changes in Predator Population Size and Structure

Few mark-recapture population estimates have been made for northern pikeminnow in the lower Snake River reservoirs. In 1993 and 1994, Ward (1997) estimated the size of the northern pikeminnow population in Lower Granite Reservoir to be between 69,651 and 81,891 fish, although these population sizes may have been biased upward by captures of fish beyond the reservoir by sport fishermen (Petersen et al. 1999). Lacking population estimates for different reservoir areas, Catch per unit effort (CPUE) was thus the primary data available for densities of northern pikeminnow. CPUE of northern pikeminnow has been shown to be well correlated with mark-recapture population estimates for a river reach (Ward et al. 1995). Bennett and Naughton (1998) found few differences in CPUE of northern pikeminnow (>200 mm) between different areas of Lower Granite Reservoir during 1996-97. CPUE ranged from about 0.2 to 1.8 fish/15 minutes in the Snake River arm. The mid-point in this range, 1.0 fish/15 minutes, would correspond to about 46 fish/rkm based on the data and methods Petersen et al.(1999) applied in the free-flowing Snake River. Except for tailrace boat-restricted zones (BRZ), which had very high CPUEs, northern pikeminnow CPUE in the lower Snake River reservoirs during 1991 (Ward et al.1995) ranged from: forebay 1-2, mid-reservoir 0-3, and tailrace 0-2. In other reservoirs of the Columbia River, tailrace and forebay zones tended to have higher densities of northern pikeminnow than mid-reservoir zones (Petersen 1994, Ward et al. 1995). Northern pikeminnow population estimates and densities (fish per rkm) for the Lower Snake River and also for John Day Reservoir where mark-recapture estimates have been made are summarized in Table 5.

Table 5. Population (mark-recapture studies) and density estimates for northern pikeminnow in reservoirs of the lower Snake River.

Reach / Year	Population estimate (95% CI)	Density (fish / rkm)	Source
Lower Granite			
1993	81,891 ¹ (50,785 - 139,389)	1,575	David Ward, Oregon Dept. Fish & Wildlife (pers. commun., 1999)
1994	69,651 ¹ (40,377 - 130,595)	1,339	
John Day (all areas)			Beamesderfer and Rieman (1991)
1984	68,947	561	
1985	84,114	684	
1986	102,888	837	

¹Population estimates for northern pikeminnow (1993 and 1997) in Lower Granite Reservoir may be biased since they include fish that may have been captured upriver by sport fishermen, beyond the reservoir (David Ward, pers. commun., 1999).

Level of Predation on Juvenile Salmon

Diet composition--Diet of northern pikeminnow varies with size (Ricker 1941, Falter 1969, Olney 1975, Buchanan et al. 1981.). In the Columbia River, invertebrates dominated the diet of fish smaller than 300 mm FL with fish and crayfish increasing in importance as size increased (Thompson 1959, Kirn et al. 1986, Poe et al. 1991, 1994). Salmonids, sculpins (*Cottus* spp.), trout perch (*Percopsis omiscomaycus*), and suckers (*Catostomus* spp.) were the most common fish prey items of northern pikeminnow (Poe et al. 1991).

The diet of northern pikeminnow in John Day Reservoir during 1983-86 is summarized in Table 6. Fish was the most important component of the diet by weight (81%); 47% of the sample consumed fish (Poe et al. 1991). Salmonids were the single most important item in the diet of the northern pikeminnow, comprising about 67% of the stomach contents by weight.

Table 6. Percent frequency of occurrence and percent by weight of prey consumed by northern pikeminnow in John Day Reservoir (all stations and months combined), 1983-1986 (Poe et al. 1991).

Prey group	Frequency of Occurrence (%)	Weight (%)
Fish	47.0	80.9
Petromyzontidae	1.1	0.2
Salmonidae	33.5	66.7
Salmon spp.	27.8	48.2
Steelhead	3.5	13.5
Unidentified	4.4	5.0
Catostomidae	1.1	1.7
Centrarchidae	0.1	0.0
Clupeidae	1.2	0.3
Cottidae	6.7	7.3
Cyprinidae	0.8	1.4
Ictaluridae	0.0	0.0
Percopsidae	3.6	2.4
Unidentified nonsalmonids	0.5	0.2
Crustacea	48.3	13.4
Cladocera	0.2	0.0
Copepoda	0.0	0.0
Amphipoda	35.5	3.4
Isopoda	0.1	0.0
Decapoda	17.1	9.9
Insecta	43.8	2.3
Diptera	13.3	0.1
Ephemeroptera	22.1	0.6
Hemiptera	2.0	0.0
Homoptera	2.4	0.0
Hymenoptera	7.1	0.3
Coleoptera	7.0	0.1
Trichoptera	1.0	0.0
Unidentified	15.6	0.9
Mollusca	3.8	0.6
Other food	15.9	2.6

The food habits of northern pikeminnow throughout the lower Columbia Basin during 1990-96 were generally consistent with those reported in other studies (Zimmerman 1997). Poe et al. (1991) found that food habits of each predator species differed between near-dam and mid-reservoir areas within John Day Reservoir, and the relative abundance of northern pikeminnow is greatest in dam tailraces (Friesen and Ward 1997, Zimmerman and Ward 1997). Differences in habitats occupied by each predator species would reduce the probability of competitive interactions within individual reservoirs. Vigg et al. (1991) reported that nonsalmonid consumption rates by northern pikeminnow were less than that of other predators in John Day Reservoir. Spatial variation in prey fish composition often reflected differences in species composition of fish communities within the lower Columbia Basin. Northern pikeminnow consumed more exotic prey fishes such as ictalurids and centrarchids in the Snake River since those species are more abundant in the Snake River (Zimmerman and Parker 1996).

Salmonid consumption rates--Salmonids were generally an important diet component only for large, old northern pikeminnow (Vigg et al. 1991) and consumption rates of juvenile salmonids by northern pikeminnow increased exponentially as size increased (Beamesderfer et al. 1996, their Fig. 3A).

Northern pikeminnow consumption rates on juvenile salmonids were highest in the McNary Dam tailrace during July corresponding to subyearling juvenile passage (Table 7 and 8; Vigg et al. 1991). Northern pikeminnow consumption rates on juvenile salmonids in the body of John Day Reservoir were high during May (abundant yearling migrants) as well as July.

Table 7. Mean daily consumption (prey/predator) of juvenile salmonids estimated for northern pikeminnow in the restricted zone (RZ) of McNary Dam tailrace and the rest of John Day Reservoir (pool), April-August 1983-1986 (Vigg et al. 1991).

Predator species and location	n	Salmonids per predator per day – by month				
		April	May	June	July	August
Northern pikeminnow						
McNary RZ	2,371	0.139	0.490	0.358	2.027	0.392
Pool	1,996	0.043	0.251	0.086	0.154	0.094

Table 8. Estimated variance of consumption rates of juvenile salmonids by northern pikeminnow in John Day Reservoir by month, 1983-1986. Consumption rates are mean number of smolts eaten per day per individual predator (from Vigg et al. 1991). The restricted zone is that portion of the tailrace immediately below McNary Dam from which boats are excluded.

Area and month	Sample size	Consumption rate	Variance
Restricted zone (RZ):			
April	242	0.14	2.3×10^{-4}
May	424	0.49	11.4×10^{-4}
June	614	0.36	14.3×10^{-4}
July	589	2.03	102.6×10^{-4}
August	502	0.40	25.2×10^{-4}
Reservoir (excluding RZ):			
April	264	0.04	1.2×10^{-4}
May	586	0.25	6.1×10^{-4}
June	469	0.09	3.2×10^{-4}
July	243	0.15	12.4×10^{-4}
August	434	0.09	4.5×10^{-4}

Consumption rates of juvenile salmonids by northern pikeminnow generally increase in areas of high salmonid abundance (Thompson 1959a, Buchanan et al. 1981, Poe et al. 1991, Vigg et al. 1991, Tabor et al. 1993). Northern pikeminnow near the dams exhibit a classical functional response where average predator consumption rates increase with increasing prey density up to a maximum corresponding to satiation (Henchman 1986, Vigg 1988, Petersen and DeAngelis 1992). However, their response in the reservoir body where most predation occurs is uncertain due to a lack of information.

Estimated Losses of Juvenile Salmonids to Predation

Research in 1983-1986 concluded that resident predator fishes consumed between 1.9 and 3.3 million juvenile salmon and steelhead (95% confidence interval) annually in John Day Reservoir alone (Rieman et al. 1991). Northern pikeminnow accounted for 78% of the losses, which would be 1.5-2.6 million fish. Individual consumption rates were low (reservoir-wide average <0.2 salmonids per predator per day based on stomach samples and digestion rate experiments: Vigg et al. 1991, Rieman et al. 1991) but the pikeminnow population was large (85,000 >250 mm FL with 95% confidence intervals of -23% to +28% based on the average for mark-recapture estimates in three years: Beamesderfer and Rieman 1991).

Petersen (1994) re-evaluated the stratification scheme used for the original loss estimates, and concluded that it was more valid to stratify the estimate by four or more reservoir areas rather than the two areas used by Rieman et al. (1991). The revised method resulted in a much reduced estimate of salmonid losses to fish predation. Petersen (1994) estimated the annual loss of juvenile salmonids to predation by northern pikeminnow in John Day Reservoir to be 1.4 million, or approximately 7.3% of all juvenile salmonids entering the reservoir.

Northern pikeminnow predation throughout the Columbia and Snake Rivers was indexed in 1990-1993 based on electrofishing catch rates of predators and the occurrence of salmonids in predator stomachs relative to estimates in John Day Reservoir (Ward et al. 1995). Northern

pikeminnow abundance was estimated to total 1,765,000 and daily consumption rates averaged 0.06 salmonids per predator (Beamesderfer et al. 1996, their Table 6). Average index values for predation losses relative to the estimate for John Day Reservoir were 808% downstream from Bonneville Dam, 275% in Bonneville and The Dalles Reservoirs combined, 50% in McNary Reservoir, 98% in Columbia River reservoirs upstream from the Snake River, and 37% in the four Lower Snake River reservoirs (Table 9). These index values would translate into 16.4 million juvenile salmon and steelhead consumed annually by northern pikeminnow based on numbers observed in John Day Reservoir (Table 6). This is 8% of the approximately 200 million hatchery and wild juvenile salmonid migrants in the system. Other work corroborates findings for the Snake River (Chandler 1993, Curet 1993) and the mid-Columbia between Priest Rapids and Chief Joseph dams (Burley and Poe 1994).

Table 9. Projected abundance of northern pikeminnow, salmonid consumption rates, and losses of juvenile salmonids to predation by northern pikeminnow based on 1983-1986 mark-recapture estimates in John Day Reservoir (Beamesderfer and Rieman 1991), estimates of predation losses (Petersen 1994), live proportion (85%) from feeding experiments (Petersen et al. 1994), and index sampling throughout the Columbia and Snake Rivers in 1990-1993 (Ward et al. 1995, Beamesderfer et al. 1996).

Location	Length (km)	Northern pikeminnow abundance (thousands)	Consumption rate (live smolts pred. ⁻¹ day ⁻¹)	Losses (millions)
Estuary-Bonneville	224	734	0.09	9.7
Bonneville Reservoir	74	208	0.03	1.0
The Dalles Reservoir	38	117	0.13	2.3
John Day Reservoir	123	85	0.09	1.2
McNary Reservoir	98	58	0.07	0.6
Priest Rapids Reservoir	29	28	0.05	0.2
Wanapum Reservoir	61	168	<0.01	0.2
Rock Island Reservoir	34	38	0.09	0.5
Rocky Reach Reservoir	68	142	<0.01	0.2
Wells Reservoir	47	39	0.01	<0.1
Ice Harbor Reservoir	51	14	0.02	<0.1
Lower Monumental Reservoir	46	53	0.01	0.1
Little Goose Reservoir	60	55	0.02	0.2
Lower Granite Reservoir	85	26	0.02	0.1
Total	1,038	1,765	0.06	16.4

Effect of Predator Removal on Predator and Prey Populations--Predation by northern pikeminnow (formerly northern squawfish) *Ptychocheilus oregonensis* was identified as a major source of mortality for juvenile salmonids *Oncorhynchus* spp. in the lower Columbia and Snake Rivers (Rieman et al. 1991, Ward et al. 1995). Control fisheries, operated by state and tribal fishery agencies, have been implemented in the Columbia Basin since 1990 to harvest northern pikeminnow with a goal of 10-20% exploitation. Rieman and Beamesderfer (1990) predicted that exploiting northern

pikeminnow greater than 275 mm fork length at a sustained annual rate of 10-20% would result in a 50% annual decrease in salmonid losses to predation.

From 1991 to 1996, three fisheries (sport-reward, dam-angling, and gillnet) harvested approximately 1.1 million northern pikeminnow greater than or equal to 250 mm fork length, with the sport-reward fishery contributing 86.5% of the total catch (Friesen and Ward 1997). Total exploitation averaged 12.0% (range 8.1-15.5) for 1991-1996 and met program goals in all years except 1993.

Gillnet and dam-angling fisheries harvested significantly larger-sized northern pikeminnow than the sport-reward fishery. Although the gillnet and dam-angling fisheries catch fewer fish, these target fisheries are important to the overall program because **each predator** captured in these fisheries reduces potential predation on juvenile salmonids to a greater extent than the average sport-caught fish. The reason for this difference in effectiveness is twofold: (1) the number of salmonids consumed by an individual pikeminnow is directly related to predator size, and (2) predation rate is higher in specific locations such as dam forebays and tailraces (Vigg et al. 1991).

Modeling results indicate that potential predation on juvenile salmonids by northern pikeminnow has decreased 25% since fishery implementation. The relative benefits of a given exploitation rate decreased with time as the number of large northern pikeminnow was reduced; however, additional reductions in potential predation are probable if exploitation is maintained at mean 1994-1996 levels. Friesen and Ward (1999) estimated a long-term reduction in potential predation of 3.8 million juvenile salmonids per year (representing 1.9% of the total population) if northern pikeminnow exploitation rates are maintained at mean levels. This estimate, however, includes predator removal in the free-flowing sections of the Hanford Reach and Snake River near Hells Canyon.

Projected estimations of system-wide percent reduction in juvenile salmonid mortality from predation by northern pikeminnow (relative to pre-1990 levels) due to the Predator Control Program is 13.0% for 1992-1999 and 14.9% for 2000 to 2006 (Table 10, D. Ward and H. Schaller, pers. commun. to PATH Hydro Work Group, 16 March 1999).

Table 10. Mid-range model estimates for percent reductions in juvenile salmonid mortality from predation by northern pikeminnow (relative to pre-1990 levels) due to the Predator Control Program, 1990-2006 (Ward and Schaller memo to the PATH Hydro Work Group, 16 March 1999).

Year	River Reach / Reservoir									System
	Below Bonn.	BON	TDA	JDA	MCN	ICE	LMO	LGO	LGR	
1990	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
1991	0.0%	0.6%	0.6%	6.5%	0.9%	0.0%	0.0%	0.0%	0.0%	0.6%
1992	2.9%	10.0%	27.2%	12.5%	2.0%	13.7%	8.3%	5.7%	0.0%	6.4%
1993	7.6%	21.7%	27.4%	18.1%	1.6%	10.7%	10.5%	12.9%	0.0%	11.5%
1994	7.8%	18.5%	27.4%	19.8%	1.3%	8.0%	9.9%	12.2%	0.0%	11.3%
1995	12.0%	17.3%	28.3%	18.6%	0.9%	5.8%	8.4%	12.8%	0.0%	14.0%
1996	15.5%	15.4%	30.9%	14.0%	0.7%	4.1%	7.8%	11.5%	0.0%	16.1%
1997	16.0%	14.8%	32.9%	13.6%	0.4%	2.7%	5.4%	12.4%	0.0%	16.5%
1998	14.1%	14.9%	29.8%	9.9%	0.3%	1.7%	3.6%	8.8%	0.0%	14.7%
1999	12.9%	15.2%	30.5%	6.8%	0.1%	0.9%	2.3%	6.1%	0.0%	13.7%
2000	13.6%	15.1%	30.6%	7.4%	0.1%	0.4%	3.1%	6.4%	0.0%	14.2%
2001	14.1%	15.0%	30.7%	8.0%	0.0%	0.2%	3.7%	6.7%	0.0%	14.6%
2002	14.5%	14.9%	30.6%	8.5%	0.0%	0.0%	4.1%	6.9%	0.0%	14.9%
2003	14.8%	14.7%	30.8%	9.0%	0.0%	0.0%	4.4%	7.0%	0.0%	15.1%
2004	15.0%	14.6%	30.8%	9.3%	0.0%	0.0%	4.6%	7.1%	0.0%	15.2%
2005	15.1%	14.5%	30.9%	9.5%	0.0%	0.0%	4.7%	7.2%	0.0%	15.3%
2006	15.1%	14.5%	30.9%	9.7%	0.0%	0.0%	4.8%	7.2%	0.0%	15.3%

Mean reductions by time period and location:										
1990-91	0.0%	0.3%	0.3%	3.3%	0.5%	0.0%	0.0%	0.0%	0.0%	0.3%
1992-99	11.1%	16.0%	29.3%	14.2%	0.9%	6.0%	7.0%	10.3%	0.0%	13.0%
2000-06	14.6%	14.8%	30.8%	8.8%	0.0%	0.1%	4.2%	6.9%	0.0%	14.9%

These simulated levels of reduction represent mid-range estimates for age 6 to 16-year-old pikeminnow. The mortality reduction estimates are derived from a spreadsheet model based on predator population size structure and the mean total pikeminnow exploitation rate estimates (David Ward, ODFW, pers. commun., 29 July 1999).

The annual system-wide reduction in pikeminnow predation is projected to level off at about 15% during 2000 to 2006 (Fig. 1). The mortality reduction below Bonneville Dam shows a similar trend and level of magnitude. The mortality reduction in the lower Columbia River

reservoirs also shows a similar trend, but a higher level of magnitude (i.e., a future projection of about 18%). The highest estimated predation mortality reductions are in The Dalles Reservoir, over 30% annual reductions during 1996-2006. Pikeminnow populations and predation on salmonids are relatively low in McNary Reservoir, with low potential for predation reductions. The three lower Snake River reservoirs were intermediate (5-11%) during 1993-1998, and are projected to level off at about 3-4% reductions for 1999 to 2006. Lower Granite has zero percent reductions due to negligible populations of northern pikeminnow. Smallmouth bass is the dominant fish predator in Lower Granite Reservoir and upstream.

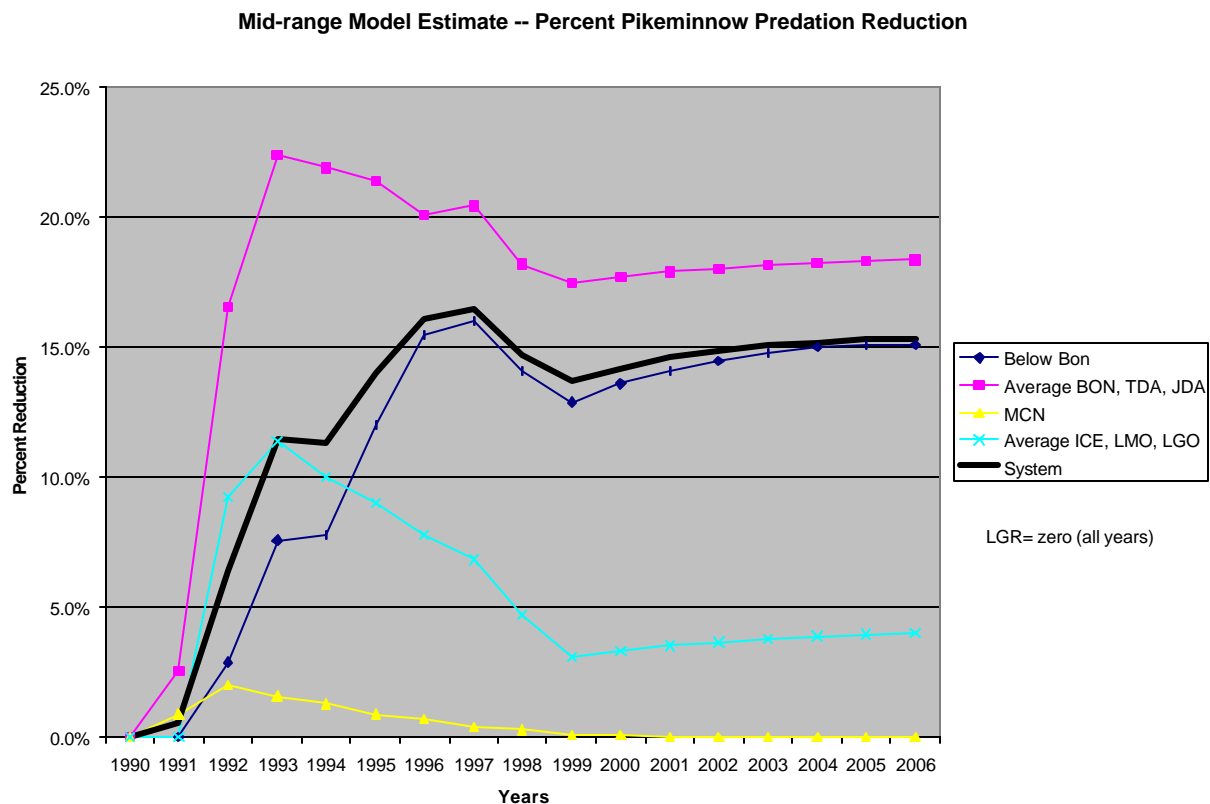


Figure 1. Estimated reduction in system-wide juvenile salmonid mortality due to northern pikeminnow predation – compared to reach components: below Bonneville, lower Columbia reservoirs (BON, TDA, JDA mean), McNary (MCN), lower Snake reservoirs (ICE, LGO, LMO mean), and Lower Granite (LGR), 1990-2006 (Ward and Schaller memo to PATH Hydro Work Group, 16 March 1999).

Intra-specific compensation--A multiyear evaluation was conducted on the biological response of predator populations to northern pikeminnow removals during 1990-1996. The investigators found no evidence that surviving northern pikeminnow populations compensated for sustained removals (Ward 1997). Indices of northern pikeminnow abundance and consumption of juvenile salmonids were consistently lower from 1994 to 1996 than from 1990 to 1993 (Zimmerman and Ward 1997). Piscivory by northern pikeminnow declined over time from 1990-1996 (Zimmerman 1997, Zimmerman and Ward 1997). No single environmental or salmonid passage variable was found to be consistently related to consumption of juvenile salmonids by northern pikeminnow. Size structure

of northern pikeminnow populations appeared to decrease in response to removals of large fish (Knutsen and Ward 1997); however, they found no trend of increased growth, fecundity, or year-class strengths.

Effect of other, non-lethal, predator control measures--The significance of selective predation and evaluation of prey protection measures for juvenile salmonids in the Columbia and Snake River reservoirs has been studied continuously since 1991 (Poe 1992). Biological criteria have been developed for the siting and operation of juvenile fish bypass systems in order to reduce fish predation (Poe et al. 1994, Shively et al. 1994a,b, 1996a,b).

Radiotelemetry has been a valuable tool for determination of northern pikeminnow distribution and potential predation relative to riverine conditions such as flow, velocity, depth and temperature (Faler et al. 1988, Shively et al. 1994a). Faler et al. (1988) observed that most northern pikeminnow were excluded from areas within the McNary Dam tailrace when water velocities exceeded 0.7 m/second.

Shively et al. (1996a) developed the following biological criteria (and their bases) for siting smolt bypass systems so that northern pikeminnow predation would be minimized:

Water velocity >1 m/second (predator swimming performance and radiotelemetry).

Distance from shore >75 m (telemetry studies and The Dalles Dam).

Water depth >10 m (telemetry studies) .

A site that satisfies two out of three criteria will generally protect smolts from northern pikeminnow predation. It is important that conditions existing considerable distance downstream from a smolt bypass outfall structure be considered, since smolts may be disoriented and vulnerable to predation for some time (distance downstream) after re-entering the river (Rip Shively, USGS, pers. commun., 29 July 1999).

In addition, the effects of high water velocity conditions on pikeminnow predator effectiveness have been evaluated in free-flowing sections of streams. Buchanan et al. (1981) reported that only 2% of the 1,127 pikeminnow examined in a free-flowing section contained salmonids in their diet. Thompson (1959) found 7.5% of 3,546 pikeminnows contained salmonids in their diet. These studies suggest that under high velocity, free-flowing conditions, pikeminnow feed mainly on benthic prey (Brown and Moyle 1981, Tabor et al. 1993).

Further, Petersen et al. (1999) recently conducted a study specifically designed to address changes in predation due to draw down flow conditions. Diet, habitat selection, and bioenergetic data were compared for free-flowing and impounded sections of the Lower Snake River, and it was concluded that draw down would decrease predation by 74 and 83% in spring and summer, respectively. This estimated decrease in predation was mainly a result of the loss of forebays and tailraces (areas where pikeminnow diets were about 80% salmonids), a switch to a diet mainly of benthic invertebrates and other fish, a decrease in smallmouth bass population, and a decrease in temperature.

Smallmouth Bass

Biological Attributes Relative to Predation on Juvenile Salmonids

Found in lakes, rivers, and streams, smallmouth bass (*Micropterus dolomieu*) have relatively large mouths that allow them to consume juvenile fish, including salmonids. In fact, by the time they are 1.5 in long, insects and small fish comprise the majority of the smallmouth bass diet (Iowa 1999). According to Bennett and Naughton (1998), smallmouth bass and salmonids utilize many of the same habitat types.

Smallmouth bass spawn in the early spring. They lay their eggs in shallow water and prefer rocky or gravel substrate. By the time the eggs hatch, salmon have begun to spawn, and the smallmouth fingerlings may be large enough to prey on newly hatched salmonids.

Changes in predator population size and structure--Absolute predation loss estimates are highly sensitive to the population size of the predators (Rieman et al. 1991, Petersen et al. 1999). Density and population estimates for smallmouth bass were based primarily on mark-recapture studies by Bennett et al. (1997), Bennett and Naughton (1998), and David Ward (pers. commun., ODFW, 1999) (Table 11). Bennett et al. (1997) estimated there were 20,911 (95% CI 17,092-26,167) smallmouth bass larger than 174 mm in Lower Granite Reservoir. Eighty percent of the population was less than 250 mm. Bennett and Naughton estimated the population for different areas within Lower Granite Reservoir and Ward estimated the bass population in Lower Monumental Reservoir. Smallmouth bass population estimates and densities (fish per rkm) for the lower Snake River and also for John Day Reservoir where mark-recapture estimates have been made are summarized in Table 11.

Table 11. Population (mark-recapture studies) and density estimates for smallmouth bass in free-flowing and reservoir portions of the lower Snake River. (Petersen et al. 1999)

Reach / Year	Population estimate (95% CI)	Density (fish / rkm)	Source
Snake River arm (transitional)	2,847 (2,231 - 3,763)	219	Bennett and Naughton (1998)
Lower Granite tailrace	2,519 (1,712 - 4,089)	420	Bennett and Naughton (1998)
Lower Granite forebay	4,884 (3,626 - 6,951)	814	Bennett and Naughton (1998)
Lower Granite reservoir	20,911 (17,092 - 26,197)	402	Bennett et al. (1997)

Lower Monumental reservoir	7,204 (5,073 - 10,594)	157	David Ward, Oregon Dept. Fish & Wildlife (pers. commun., 1999)
John Day Reservoir			Beamesderfer and Rieman (1991)
1985	31,948	260	
1986	37,959	309	

Level of Predation on Juvenile Salmon

Diet composition--The food habits of smallmouth bass throughout the lower Columbia Basin during 1990-1996 were generally consistent with those reported in previous studies (Zimmerman 1997). The primary prey of adult smallmouth bass throughout their range are crayfish and fish (Scott and Crossman 1973, Carlander 1977, Austen and Orth 1985, Roell and Orth 1993).

The diet of smallmouth bass in John Day Reservoir during 1983-1986 is summarized in Table 12. Fish was the most important component of the diet by weight (78%) and 61% of the

Table 12. Percent frequency of occurrence and percent by weight of prey consumed by smallmouth bass in John Day Reservoir (all stations and months combined), 1983-1986 (Poe et al. 1991).

Prey group	Frequency of Occurrence (%)	Weight (%)
Fish	60.7	77.6
Petromyzontidae	0.0	0.0
Salmonidae	4.0	4.2
Salmon spp.	1.5	2.5
Steelhead	0.0	0.0
Unidentified	2.5	1.7
Catostomidae	12.3	22.6
Centrarchidae	1.1	0.5
Clupeidae	0.0	0.0
Cottidae	27.4	32.5
Cyprinidae	6.8	11.6
Ictaluridae	0.1	0.1
Percopsidae	6.3	5.0
Unidentified nonsalmonids	10.8	1.0
Crustacea	60.3	21.3

Cladocera	5.0	0.0
Copepoda	2.1	0.0
Amphipoda	34.0	0.5
Isopoda	0.2	0.0
Decapoda	33.6	20.7
Insecta	36.8	0.6
Diptera	19.8	0.1
Ephemeroptera	12.4	0.3
Hemiptera	1.1	0.0
Homoptera	1.1	0.0
Hymenoptera	3.2	0.1
Coleoptera	1.5	0.0
Trichoptera	1.7	0.0
Unidentified	5.4	0.1
Mollusca	0.7	0.0
Other food	13.1	0.1

sample consumed fish (Poe et al. 1991). Cottidae (sculpins) and catostomidae (suckers) were the two most important item in the diet of the smallmouth bass, together comprising about 55% of the stomach contents by weight. Salmonids comprised about 4.2% of the stomach contents by weight.

Smallmouth bass preyed on sculpins, suckers, cyprinids, sand rollers, and crayfish to a greater extent (by weight and frequency of occurrence) than did northern pikeminnow in John Day Reservoir (Poe et al. 1991). Smallmouth bass consumed far fewer juvenile salmonids than did northern pikeminnow throughout the study area (Zimmerman 1997), consistent with their diets and consumption rates of salmonid and nonsalmonid prey in John Day Reservoir (Poe et al. 1991, Vigg et al. 1991). Estimated daily consumption rates of smallmouth bass on cottids and cyprinids generally exceeded consumption rates on salmonids (Ward and Zimmerman 1997). Nevertheless, smallmouth bass consumption rates exceeded one juvenile salmonid/predator/day in specific areas in summer (Tabor et al. 1993, Ward and Zimmerman 1997), when subyearling chinook salmon are the only available salmonid prey.

Poe et al. (1991) found that food habits of each predator species differed between near-dam and mid-reservoir areas within John Day Reservoir. Smallmouth bass are generally relatively more abundant in dam forebays than tailraces. Vigg et al. (1991) reported that nonsalmonid consumption rates by smallmouth bass were much greater than that for northern pikeminnow in John Day Reservoir. Spatial variation in prey fish composition in the diet of smallmouth bass reflected differences in species composition of fish communities within the lower Columbia Basin (Zimmerman 1997). Trends in differential predation on resident fishes were most evident for smallmouth bass because they consumed nonsalmonids to a much greater extent than did northern pikeminnow. Smallmouth bass consumed a

higher percentage of ictalurids and centrarchids in the Snake River, where those non-native prey fish are more abundant compared to the lower Columbia River (Zimmerman and Parker 1996). Predation on sand rollers and threespine stickleback was restricted to the lower Columbia River. Non-targeted species were recorded while electrofishing for predators, and catch rates of sand rollers and threespine stickleback were greatest downstream from Bonneville Dam.

Smallmouth bass consumed smaller chinook salmon in spring than did northern pikeminnow, and consumed far more subyearling chinook salmon in summer than yearling chinook salmon in spring (Zimmerman 1997). Smallmouth bass were capable of ingesting much larger prey (including a 241 mm cyprinid), and their feeding activity was similar between spring and summer, based upon the frequency of occurrence of food items (Zimmerman 1997). Consequently, predator-prey size relationships may reflect the degree and timing of habitat overlap as suggested by Tabor et al. (1993), who attributed high levels of smallmouth bass predation on subyearling chinook salmon to overlap of rearing habitat of subyearling chinook with the preferred habitats of smallmouth bass in summer. Skewed length distributions of juvenile salmonid prey might also result from size-related vulnerability of prey, for example, associated with swimming speed (Poe et al. 1991). Alternatively, size distributions of salmonids collected in juvenile bypass systems may not have been representative of sizes of salmonids available to resident predators. Regardless of the mechanism, an important consequence of size-selective predation would be increased vulnerability of wild juvenile salmonids, which are smaller than chinook salmon and steelhead reared in hatcheries (Zimmerman 1997).

Salmonid consumption rates--Consumption rates for smallmouth bass were not estimated in McNary Dam tailrace due to low number present and inadequate sample size (Tables 13 and 14). The highest consumption rates of juvenile salmonids by smallmouth bass occurred during July in John Day Pool – 0.118 salmonids per predator per day.

Table 13. Mean daily consumption (prey/predator) of juvenile salmonids estimated for smallmouth bass in the restricted zone (RZ) of McNary Dam tailrace and the rest of John Day Reservoir (pool), April-August 1983-1986 (Vigg et al. 1991).

Predator species and location		Salmonids per predator per day – by month				
	n	April	May	June	July	August
Smallmouth bass (>200 mm)						
McNary RZ	24	--	--	--	--	--
Pool	2,856	0.003	0.009	0.019	0.118	0.070

Table 14. Estimated variance for consumption rates of juvenile salmonids by smallmouth bass in John Day Reservoir by month, 1983-1986. Consumption rates are mean number of smolts eaten per day per individual predator (Vigg et al. 1991).

Area ^a and month	Sample size	Consumption rate	Variance
Reservoir (excluding RZ)			
April	293	<0.01	0.1×10^{-4}
May	673	0.01	0.3×10^{-4}
June	793	0.02	0.5×10^{-4}
July	608	0.12	2.2×10^{-4}
August	489	0.07	7.2×10^{-4}

^a Estimates for smallmouth bass do not include the boat-restricted zone because few fish of this species were collected there. The restricted zone (RZ) is that portion of the tailrace immediately below McNary Dam from which boats are excluded.

Estimated losses of juvenile salmonids to predation--Rieman et al. (1991) estimated losses of juvenile salmonids to fish predators in John Day Reservoir based on field studies conducted during 1983-1986. Smallmouth bass accounted for 9% of the total, which would be 170,000 and 300,000 salmonids per year, based on the total fish predation loss estimate of between 1.9 and 3.3 million juvenile salmon and steelhead (95% confidence interval). These predation loss estimates have a high degree of uncertainty in various steps of the estimation methodology and therefore should be interpreted with caution. Using the same data base, but with a different stratification scheme for the loss calculation, Petersen et al. (1994) estimated the total annual loss to predation at 1.4 million fish (i.e., only about 52% of the mean loss of 2.7 million juvenile salmonids estimated by Rieman et al. (1991)).

Effect of predator removal on smallmouth bass populations --A multiyear evaluation was conducted on the biological response of predator populations to northern pikeminnow removals during 1990-1996. The investigators found no evidence of smallmouth bass response to sustained removals of northern pikeminnow. No trends in smallmouth bass density, consumption of juvenile salmonids, population structure, growth, mortality, or year-class strength have been realized concurrent with the Northern Squawfish Management Program (Ward and Zimmerman 1997). Diets of smallmouth bass varied from year to year; however, statistical analyses did not detect any significant responses to the sustained removals of northern pikeminnow (Zimmerman 1997). Piscivory and salmonid predation varied annually for smallmouth bass but did not increase coincident with removals of northern pikeminnow. Consumption rates of non-salmonid prey fishes by smallmouth bass exceeded consumption rates by northern pikeminnow (Zimmerman 1997).

Walleye

Biological Attributes Relative to Predation on Juvenile Salmonids

As the largest member of the perch family, walleye (*Stizostedion vitreum*) can grow to 20 lb (Iowa 1999). Walleye have been shown to eat smolts of Pacific salmon and therefore pose a threat to these already declining species in the Columbia River Basin (Dentler 1993). McMahon and Bennett (1996) estimated that walleye predation may account for 2 million smolts, one third of total predation loss.

Walleye spawn in spring, shortly after the ice melts. They prefer shallow, clean, gravel bottoms to deposit their eggs. Generally, a large female is surrounded by many smaller males while her eggs are released (Iowa 1999). In their native habitats of the eastern United States, walleye and salmonids utilize different habitats, so predation does not cause a serious impact on juvenile salmonids. However, in western reservoirs, where introductions have taken place, the lack of a strong thermocline, and a small littoral zone, does not allow for this separation (McMahon and Bennett 1996).

Changes in Predator Population Size and Structure

Walleye appeared in Lake Roosevelt in 1973, (Nelson et al. 1985). At this time, yellow perch outnumbered walleye 2:1, however, just ten years later, walleye outnumbered yellow perch 3:1 (Nelson et al. 1985). According to Griffith and Scholz (1990), 714, 1,303, and 1,137 walleye were collected via electrofishing and gillnetting in 1988, 1989, and 1990, respectively.

Level of Predation on Juvenile Salmon

Diet composition--The diet of walleye in John Day Reservoir during 1983-1986 is summarized in Table 15. Fish was the most important component of the diet by weight (99.7%), while 96.4% of the sample consumed fish (Poe et al. 1991). Catostomids (suckers) were the single most important item in the diet of the walleye, comprising about 40% of the stomach contents by weight. Salmonids comprised about 13.5% of the stomach contents by weight.

The food habits of walleyes throughout the lower Columbia Basin during 1990-1996 were generally consistent with those reported in previous studies (Zimmerman 1997). Walleye diets were dominated (by weight and frequency of occurrence) by fish prey, particularly nonsalmonids. Cyprinids, catostomids, sand rollers, and cottids comprised 84% (by weight) of the total diet of walleyes in John Day Reservoir (Poe et al. 1991). During 1990-1996, walleyes consumed far fewer juvenile salmonids than did northern pikeminnow throughout the study area (Zimmerman 1997), consistent with their diets and consumption rates on salmonid and nonsalmonid prey in John Day Reservoir (Poe et al. 1991, Vigg et al. 1991). Poe et al. (1991) found that food habits of each predator species differed between near-dam and mid-reservoir areas within John Day Reservoir. Relative abundance of walleyes is greatest in dam tailraces (Friesen and Ward 1997, Zimmerman and Ward 1997).

Table 15. Percent frequency of occurrence and percent by weight of prey consumed by walleyes in John Day Reservoir (all stations and months combined), 1983-1986 (Poe et al. 1991).

Prey group	Frequency of Occurrence (%)	Weight (%)
Fish	96.4	99.7
Petromyzontidae	0.0	0.0
Salmonidae	20.7	13.5
Salmon spp.	10.8	8.3
Steelhead	0.9	2.3
Unidentified	12.3	2.7
Catostomidae	27.5	40.1
Centrarchidae	0.0	0.0
Clupeidae	0.0	0.0
Cottidae	22.0	15.9
Cyprinidae	12.4	11.3
Ictaluridae	0.3	0.1
Percopsidae	27.3	16.7
Unidentified nonsalmonids	21.6	1.9
Crustacea	8.6	0.0
Cladocera	0.0	0.0
Copepoda	0.1	0.0
Amphipoda	8.3	0.0
Isopoda	0.0	0.0
Decapoda	0.1	0.0
Insecta	11.8	0.0
Diptera	3.5	0.0
Ephemeroptera	6.4	0.0
Hemiptera	0.1	0.0
Homoptera	0.5	0.0
Hymenoptera	0.0	0.0
Coleoptera	0.9	0.0
Trichoptera	0.9	0.0
Unidentified	1.6	0.0
Mollusca	0.7	0.0
Other food	9.0	0.1

Although prey types utilized by walleyes in areas away from dams were under-represented, the impact of predation on those prey types would be relatively low because of low predator abundance. Differences in habitats occupied by each predator species would reduce the probability of competitive interactions within individual reservoirs. Nonsalmonid consumption rates by walleye were similar to smallmouth bass and greater than northern pikeminnow in John Day Reservoir (Vigg et al. 1991).

Potential impacts of walleye predation may be high, but are dependent upon annual changes in abundance to a greater extent than other predator species. Walleye abundance in John Day Reservoir from 1983-1986 was approximately 30% of smallmouth bass abundance; however, walleye abundance fluctuates widely with year-class strength (Beamesderfer and Rieman 1991, Friesen and Ward 1997).

Salmonid consumption rates--Consumption rates for walleye were not estimated in McNary Dam tailrace due to low number present and inadequate sample size (Tables 16 and 17). The highest consumption rates of juvenile salmonids by walleye occurred during July in John Day Pool, 0.447 salmonids per predator per day.

Table 16. Mean daily consumption (prey/predator) of juvenile salmonids estimated for walleye in the restricted zone (RZ) of McNary Dam tailrace and the rest of John Day Reservoir (pool), April-August 1983-1986 (Vigg et al. 1991).

Predator species and location	n	Salmonids per predator per day – by month				
		April	May	June	July	August
Walleye (all sizes)						
McNary RZ	28	--	--	--	--	--
Pool	1,021	0.021	0.113	0.118	0.447	0.232

Table 17. Estimated consumption rates of juvenile salmonids by walleye in John Day Reservoir by month, 1983-1986. Consumption rates are mean number of smolts eaten per day per individual predator (Vigg et al. 1991).

Area ^a and month	Sample size	Consumption rate	Variance
Reservoir (excluding RZ)			
April	231	0.02	0.9×10^{-4}
May	384	0.11	10.2×10^{-4}
June	297	0.12	11.4×10^{-4}
July	70	0.41	197.4×10^{-4}
August	77	0.21	83.9×10^{-4}

^a Estimates for walleyes and smallmouth bass do not include the boat-restricted zone because few fish of this species were collected there. The restricted zone (RZ) is that portion of the tailrace immediately below McNary Dam from which boats are excluded.

Estimated losses of juvenile salmonids to walleye predation--Rieman et al. (1991) estimated losses of juvenile salmonids to fish predators in John Day Reservoir based on field studies conducted during 1983-1986. Walleye accounted for 13% of the total, which would be between 250,000 and 430,000 salmonids per year based on the total fish predation loss estimate of between 1.9 and 3.3 million juvenile salmon and steelhead (95% confidence interval). These predation loss estimates have a high degree of uncertainty in various steps of the estimation methodology, and therefore should be interpreted with caution. Using the same data base, but with a different

stratification scheme for the loss calculation, Petersen et al. (1994) estimated the total annual loss to predation at 1.4 million (i.e., only about 52% of the mean loss of 2.7 million juvenile salmonids estimated by Rieman et al. (1991)).

Effect of predator removal on walleye populations--A multiyear evaluation was conducted on the biological response of predator populations to northern pikeminnow removals during 1990-1996. The investigators found no evidence of walleye response to sustained removals of northern pikeminnow (Ward 1997). Variations in walleye density and population structure appear to be driven by variations in year-class strength, not by response to removals of northern pikeminnow. No trends in growth or mortality of walleye were detected (Friesen and Ward 1997). Diets of walleye varied from year to year, however, statistical analyses did not detect any significant relationships to the sustained removals of northern pikeminnow (Zimmerman 1997). Piscivory and salmonid predation varied annually for walleye but did not increase coincident with removals of northern pikeminnow. Consumption rates of non-salmonid prey fishes by walleye exceeded consumption rates by northern pikeminnow (Zimmerman 1997).

Channel Catfish

Biological Attributes Relative to Predation on Juvenile Salmonids

Channel catfish (*Ictalurus punctatus*) are not native to the Columbia River Basin. They can grow to be 35 lb. They are omnivorous and opportunistic in feeding, and have been known to eat almost anything, dead or alive. The large channel catfish feed almost exclusively on fish.

Spawning occurs near protective cover from May to July, when water is warm. Once the eggs hatch, the young travel in schools for weeks (Iowa 1999). During this early life stage, large numbers of juvenile catfish can be consumed by larger fish.

Changes in Predator Population Size and Structure

Reliable channel catfish population estimates are not available for lower Snake River or Columbia River reservoirs. Gill-net information, however, suggests that catfish are highly abundant from Lower Granite Reservoir on the Snake River to McNary Dam on the lower Columbia River (Zimmerman and Parker 1996). Catfish were rare in the Columbia River reservoirs.

Level of Predation on Juvenile Salmon

Diet composition--The diet of channel catfish in John Day Reservoir during 1983-1986 is summarized in Table 18. Fish was the most important component of the diet by weight(68.3%); 48.8% of the sample consumed fish (Poe et al. 1991). Salmonids were the single most important item in the diet of the channel catfish, comprising about 33% of the stomach contents by weight.

Table 18. Percent frequency of occurrence and percent by weight of prey consumed by channel catfish in John Day Reservoir (all stations and months combined), 1983-1986 (Poe et al. 1991).

Prey group	Frequency of Occurrence (%)	Weight (%)
Fish	48.8	68.3
Petromyzontidae	0.1	0.0
Salmonidae	18.9	32.9
Salmon spp.	6.5	13.6
Steelhead	1.3	4.5
Unidentified	13.7	14.6
Catostomidae	1.7	3.2
Centrarchidae	0.1	0.1
Clupeidae	0.0	0.0
Cottidae	15.5	19.4
Cyprinidae	3.1	5.2
Ictaluridae	0.1	0.0
Percopsidae	2.3	0.5
Unidentified nonsalmonids	10.9	4.2
Crustacea	65.3	18.4
Cladocera	0.0	0.0
Copepoda	0.1	0.2
Amphipoda	42.4	0.0
Isopoda	0.3	18.1
Decapoda	31.0	0.9
Insecta	34.4	0.2
Diptera	10.5	0.5
Ephemeroptera	21.9	0.0
Hemiptera	0.1	0.0
Homoptera	0.3	0.0
Hymenoptera	1.7	0.0
Coleoptera	1.7	0.0
Trichoptera	1.5	0.0
Unidentified	2.3	0.2
Mollusca	9.7	5.2
Other food	29.2	7.0

Salmonid consumption rates--Consumption rates for channel catfish were much higher in McNary Dam tailrace than John Day pool (Table 19). The highest consumption rates of juvenile salmonids occurred during July-August in the tailrace, 1.4 salmonids per predator per day.

Table 19. Mean daily consumption (prey/predator) of juvenile salmonids estimated for channel catfish in the restricted zone (RZ) of McNary Dam tailrace and the rest of John Day Reservoir (pool), April-August 1983-1986 (Vigg et al. 1991).

Predator species and location	n	Salmonids per predator per day – by month				
		April	May	June	July	August
Channel catfish (all sizes)						
McNary RZ	394	0.149	0.283	0.162		1.385
Pool	262	0.065	0.078	0.054		0.000

Estimated losses of juvenile salmonids to predation--No estimates of losses of juvenile salmonids to channel catfish predation have been developed.

Pacific Lamprey

Biological Attributes Relative to Predation on Juvenile Salmonids

Pacific lamprey (*Lampetra tridentata*) are a parasitic, anadromous species. They can reach up to 1 m in length. Pacific lamprey are a predator to not only juvenile salmonids, but adults as well. They feed by attaching to other fish with their sucking mouths; they rub holes in the skin with their tongues and then suck out blood and body fluids by secreting an anticoagulant. Pacific lamprey feed on adult and young salmonids in this manner.

Anadromous Pacific lamprey spawn and die in fresh water, but spend the majority of their mature lives in the Pacific Ocean. They spawn from April through July (Moyle 1976). They prefer to disperse their eggs in mostly gravel and rocky substrates (Moyle 1976), and in riffles where the current is swift. Ammocoetes (larval lamprey) are filter feeders, subsisting on algae and organic matter (Moyle 1976).

Changes in Predator Population Size and Structure

Pacific lamprey in the Columbia River Basin have been discussed as potentially being listed as threatened or endangered. They are not now listed; however, they are thought to have extremely small populations in the upper Columbia and Snake River tributaries (Close et al. 1995), if any exist at all. Population declines of Pacific lamprey are due to reasons similar to those for population declines in salmonids. Hydropower developments along the Columbia River impede the migration and survival of this species, and due to low population levels, Pacific lamprey are not currently considered a significant source of predation on salmonids.

Yellow Perch

Biological Attributes Relative to Predation on Juvenile Salmonids

Yellow perch (*Perca flavescens*) can grow to about 1 lb. This species travels in schools and feeds on small fish and insects (Coots 1966).

Changes in Predator Population Size and Structure

Between the years 1980 and 1983, over 80% of the yellow perch captured in bottom gill-nets at Lake Roosevelt were age class IV or younger (Nelson et al. 1985).

Level of Predation on Juvenile Salmon

Diet composition--Yellow perch feed on small fish, insects, and crayfish. While Table 20 does not show fish consumption, according to Nelson et al. (1985), yellow perch do consume fish.

Table 20. Mean number and percent composition of prey items per stomach of yellow perch in Lake Roosevelt, 1982 (Nelson et al. 1985).

Prey	Mean Number	Percent Composition
Cladocerans		
<i>Daphnia</i>	0.37	9.7
<i>Diaphanosoma</i>		
<i>Ceriodaphnia</i>	0.03	0.7
<i>Leptodora</i>	0.03	0.7
<i>Chydorus</i>		
<i>Bosmina</i>	0.12	3.1
Copepods		
Calanoids	1.85	49.0
Cyclopoids	1.08	28.6
Nauplii	0.05	1.3
Rotifers	0.01	0.3
Unidentified	0.23	6.0
Sample Size	482	
Empty	17	3.5
Length Range (mm)	4-27	

Largemouth Bass

Biological Attributes Relative to Predation on Juvenile Salmonids

Largemouth bass (*Micropterus salmoides*) are a rather streamlined member of the sunfish family. This species is named for its unusually large mouth. At full growth, some largemouth bass can reach 15 lb (Minckley 1973). Largemouth are known to feed on almost anything. Largemouth bass were introduced into the Columbia River Basin (Wydoski and Whitney 1979). Minckley (1973) noted that introduced bass usually affect populations of small, native fishes through predation, sometimes resulting in the decline or extinction of such species.

Largemouth bass begin spawning in early may and end in June. They prefer to deposit their eggs on muddy or grassy bottoms in fairly shallow water (Minckley 1973).

Northern Pike

Biological Attributes Relative to Predation on Juvenile Salmonids

The northern pike (*Esox lucius*) has a relatively long mouth with several canine teeth. It is known as one of the most predatory fishes in fresh water (Iowa1999). This species can attain weights over 30 lb, and lengths up to 4 ft. According to He and Kitchell (1990), this piscivorous fish has been shown to significantly reduce prey density, and has the potential to cause large-scale changes in fish communities. Northern pike may be responsible for declines of native salmonids in Montana (McMahon and Bennett 1996). Impacts of northern pike can be either direct, such as predation, or indirect, such as forcing prey fish to alter their behavior (He and Kitchell, 1990).

Northern pike spawn in the early spring, just after the ice melts in the lakes and streams. They prefer to deposit their eggs in shallow, marshy areas of streams or grassy areas in lakes. The young remain in this area until they reach about 6 in, by which time they are feeding on other small fish (Iowa1999).

Bull Trout

Biological Attributes Relative to Predation on Juvenile Salmonids

Bull trout (*Salvelinus confluentus*) are listed as endangered in the Columbia River Basin by the Federal government.

Level of Predation on Juvenile Salmon

Salmonid consumption rates--Bull trout are piscivorous, and once had a bounty on them because of the amount of young salmon and steelhead they consumed. However, because of their low population levels, they are not currently regarded as having a significant impact on salmonid populations. Bull trout do not begin to feed on fish until approximately age III; up to that point, they consume mainly invertebrates.

Effects of Temperature on Fish Predation and Bioenergetics

The following discussion of the effects of temperature on northern pikeminnow consumption and bioenergetics is extracted from Petersen and Ward (in press).

Bioenergetic Equations and Parameters

The general balanced equation for energy is:

Growth = Consumption - Respiration - (Egestion and Excretion).

Petersen and Ward (in press) expanded components of this equation using the modeling approach and software of Hanson et al. (1997).

Consumption (C), the amount of food consumed by the fish, has the general form:

$$C = C_{\max} * p\text{-value} * F(T)$$

where:

C_{\max} = maximum specific consumption rate ($\text{g prey} \cdot \text{g predator}^{-1} \cdot \text{d}^{-1}$)

p-value = proportion (0 - 1.0) of maximum consumption C_{\max}

T = temperature ($^{\circ}\text{C}$)

$F(T)$ = the temperature dependence function.

C_{\max} was defined as an allometric function of predator mass:

$$C_{\max} = \alpha W^{\beta}$$

where:

W = fish mass (g)

α = intercept of the allometric function for consumption, and

β = slope of the allometric function for consumption.

To estimate the allometric parameters for C_{\max} , Petersen and Ward (in press) used consumption and size data from Vigg and Burley (1991), who conducted laboratory feeding experiments with northern pikeminnow preying on juvenile chinook salmon. Petersen and Ward (in press) used the maximum consumption for three size groups (501-1,100 g, 1,101-1,500 g, and 1,501-2,000 g) of northern pikeminnow preying on live salmonids at 21.5°C (Vigg and Burley 1991, their Table 2). This is near the optimum temperature for feeding and digestion for this species (Black 1953, Beyer et al. 1988, Vigg and Burley 1991). Allometric parameters were estimated by regressing the

\log_e average ration plus 1 standard deviation on the \log_e midpoints of the mass range (800 g, 1,300 g, 1,750 g; average mass for each group was not reported by Vigg and Burley 1991). Petersen and Ward (in press) used ration + 1 standard deviation for C_{\max} since only juvenile salmonid prey were used in the experiments of Vigg and Burley (1991), whereas most C_{\max} experiments use pellets or relatively inactive prey (e.g., Brett 1971, Stewart et al. 1983). Use of large, active prey like salmonids would likely underestimate the maximum ration, compared to pellets or inactive prey, because of higher rates of prey escape and occasional regurgitation (Gadomski and Hall-Griswold 1992, Petersen et al. 1994). The fitted allometric equation was:

$$C_{\max} = 0.278 W^{-0.197} \quad r^2 = 96\%; \quad N = 3.$$

Coefficients of the C_{\max} equation are similar to estimates for other large, predators such as smallmouth bass ($\alpha=0.25$; $\beta=-0.31$), walleye ($\alpha=0.25$; $\beta=-0.27$), and northern pike ($\alpha=0.2045$; $\beta=-0.18$), tabulated in Hewett and Johnson (1992) and Hanson et al. (1997). Using the average ration from Vigg and Burley (1991), and not adding 1 standard deviation to the average, produced a much poorer fit to mass ($r^2 = 10\%$; $N = 3$).

Petersen and Ward (in press) modeled the temperature dependence function of consumption $F(T)$ using Thornton and Lessem's (1978) approach. This combines increasing and decreasing logistic equations to produce a dome-shape function of consumption versus temperature.

Vigg and Burley (1991) derived parameters for the Thornton and Lessem model for northern pikeminnow, except for the low optimum temperature (CTO) and the high optimum temperature (CTM, their Table 2), which Petersen and Ward (in press) estimated using an iterative search method. Petersen and Ward first calculated the maximum consumption rate at the optimum temperature (21.5 °C) using the best-fit temperature-dependent equation of Vigg and Burley (their equation 5). Parameters CTO and CTM were found by iteratively searching for a higher temperature (CTO) and a lower temperature (CTM) that produced a consumption rate 2% above or below the computed maximum rate.

Activity-dependent respiration (R), the amount of energy in mass equivalents of oxygen necessary to carry out standard and active metabolism, was modeled as:

$$R = R_s \bullet ACT$$

where:

$$R_s = \text{Standard metabolism (g O}_2 \bullet \text{ g}^{-1} \bullet \text{ d}^{-1})$$

ACT = the multiplicative increment for active metabolism.

To estimate standard metabolism, Petersen and Ward (in press) used the model:

$$R_s = aW^b \bullet e^{\tau T}$$

where:

W = fish mass (g),

T = temperature (°C),

a = intercept of the allometric function for respiration,

b = slope of the allometric function for respiration, and

τ = the slope of the function for temperature effects on respiration rate.

This model has been used for a variety of large predators in cool-water systems (Rice et al. 1983, Stewart et al. 1983, Hewett and Johnson 1992). Petersen and Ward (in press) used parameter values for a, b, and τ from Cech et al. (1994a,b), estimated for northern pikeminnow from the Columbia River (Petersen and Ward, in press, their Table 1).

Critical Uncertainties and Key Issues

One decade ago, participants at a predation modeling workshop scored factors affecting resident fish predation on juvenile salmonids, and the reliability of the existing information (Fickeisen et al. 1989). The ranking (number of votes) was only relative, and no attempt was made during the workshop to provide an absolute evaluation of the importance of the various factors to an understanding of predator-prey dynamics. Table 21 provides a comprehensive list of these factors and reflects the progress that has, and in some cases has not, been made toward reducing uncertainty.

Table 21. Factors that may influence fish predation on juvenile salmonids; entries are grouped and listed by relative importance, as indicated by vote of workshop participants (Fickeisen et al. 1989).

Popularity Score (a)	Current Knowledge (1989) (b)	Factor
18	None	Residence time
12	None	Prey condition
11	Some	Size structure of prey
10	Unknown	Predator distribution with respect to prey -- spatial & temporal
10	None	Inter-specific (compensatory relationships) and intra-specific interactions (e.g., cannibalism)
10	Some	Size structure of predators
9	None	Prey numbers
7	Unknown	Flow
7	None	Route of passage through dam
6	None	Wild versus hatchery stock
5	Substantial	Predator population
5	Some	Species of prey
4	None	Disease
3	Substantial	Growth rate of predators
3	Some	Temperature
2	Substantial	Species of predators
2	Substantial	Prey timing
2	Substantial	Predator mortality
1	Unknown	Transportation
1	Unknown	Origin of smolts (how far upstream?)
1	None	Visibility/turbidity

1	Some	Spawning activity of predators
1	Some	Shore habitat
1	Some	Fecundity of predators (year class, population dynamics)
0	Unknown	Power peaking
0	None	Alternative mortality of prey within reservoir (e.g., disease, nutrition, DO, residualization)
0	Some	Preconditioning of prey
0	Some	Effect of spill
0	Some	Alternative food sources

(a) Number of votes each received – each participant had seven votes; multiple votes for a single issue were allowed.

(b) Status of knowledge of the factor as it relates to predation in the Columbia River.

Current Uncertainties

- C A detailed understanding of how hydrosystem configuration affects fish predation dynamics is lacking – both in terms of the historical development of the FCRPS to its current state and major proposed changes for the future. Refer to Petersen et al. (1999) for a quantitative assessment of the potential effects of dam breaching on fish predation in the Lower Snake River.
- C Channel catfish are significant fish predators in the tailraces of dams; however, since population abundances are not quantified, their contribution to overall system-wide losses of juvenile salmonids to predation is not known.
- C Channel catfish, walleye, and smallmouth bass are significant predators on juvenile salmonids, but the effectiveness of potential control measures such as basin-wide changes in sport fishing regulations has not been adequately tested; also, some measures may not be feasible due to political constraints.
- C The role of fish predation on flow-temperature-salmonid survival relationships in the Columbia River system is not well understood (e.g., smallmouth bass in Lower Granite reservoir, channel catfish in dam tailraces, and northern squawfish below Bonneville Dam).
- C The role of fish predator abundance and distribution on smolt collection efficiencies at turbine intake structures at various projects in the FCRPS is not well understood (e.g., northern pikeminnow at Bonneville Dam Second Powerhouse).
- C What are the relative biological benefits (in terms of adult salmon returns) of reduced fish predation levels in each reach of the Columbia River and at each project in the FCRPS. For example, the cost-effectiveness of piscine predator removal is probably significantly different in major tributaries, versus free-flowing reaches, versus Lower Snake reservoirs, versus Bonneville to McNary Dam, versus below Bonneville Dam, versus the estuary.

- C How would fish predation levels on juvenile salmonids be changed if the Lower Snake River dams were breached (refer to Petersen et al. 1999).
- C A key issue that has been identified for decades, but remains a problem, is reduction of fish predation in the immediate forebay and tailraces of projects - the points at which predator concentrations are typically highest as a direct result of FCRPS projects.
- C The effects of dam operations on levels of fish predation is a critical uncertainty; for example, the effects of spill volume, spill patterns, and spill duration (e.g., 12 hour or 24 hour) on forebay and tailrace survival. Issues include delay of smolts and vulnerability to predators due to structures, back-eddies, disorientation of smolts.
- C Numerous studies have shown how hatchery releases can cause functional and aggregation responses in predators. What is not known is how to translate these dynamic changes into predation losses (of hatchery and wild fish) or general statements regarding the effects of current hatchery practices and how current practices should be changed.

Key Issue: Juvenile Salmonids Lost to Fish Predation Would Have Died of other Causes before Reaching the Ocean; Therefore, Predator Control Results in No New Gain

Consumption estimates do not appear to be confounded by dam passage mortality; Petersen et al. (1994) found that 78% of juvenile salmonids eaten by northern pikeminnow near a dam were consumed while alive. Ward et al. (1995) estimated that 48% of predation occurs in mid-reservoir areas away from dams, where juvenile salmonids are presumably alive and uninjured when consumed. Of the estimated 200 million juvenile salmonids emigrating annually through the lower Columbia and Snake Rivers, approximately 16.4 million (8%) are consumed by northern pikeminnow (Beamesderfer et al. 1996).

Key Issue: Predators Eat Predominantly Dead Smolts Killed During Dam Passage

Estimates of predation losses were relatively unbiased by consumption of salmonids killed or injured by dam passage (Beamesderfer et al. 1996). Passage mortality is a major source of freshwater mortality which could confound estimates of predator effects on migrant survival if many of the salmonids eaten by predators were scavenged from those killed by dam turbines. However, most of the salmonids eaten by northern pikeminnow were eaten alive, despite observed preferences for dead salmonids in laboratory and field tests (Gadomski and Hall-Griswold 1992, Petersen et al. 1994). Petersen et al. (1994) marked and released dead and live salmonids into a dam tailrace in a 10% dead proportion that equaled the turbine mortality rate and observed that 22% of the marked salmonids subsequently recovered from northern pikeminnow stomachs were dead before release. If dead fish constitute 22% of northern pikeminnow prey near a dam, if dam effects extend 10 km upstream and downstream, and if 69% of predation occurs in that zone (Petersen 1994), then 85% of the estimated predation would be on live fish ($1 - (0.69 \times 0.22)$).

Key Issue: Predation Loss Estimates Are Not Precise or Accurate

Beamesderfer et al. (1996) reviewed methodology and assumptions comprising the loss estimates and concluded that the calculations were conservative. Uncertainty in estimates of predation losses was calculated by Rieman et al. (1991) at $\pm 25\%$ (95% confidence intervals) based on inherent sampling variability in parameter estimates. Approximate 95% confidence intervals (based on ± 2 SE) would be $\pm 60\%$ for restratified predation estimates by Petersen (1994). Assumptions about northern pikeminnow distribution, movements, and area-specific catchabilities could result in a fivefold underestimation of abundance of pikeminnow and losses of salmonids (Beamesderfer and Rieman 1988, 1991). Estimates of predation losses based on examination of stomach contents could also be conservative because pikeminnow kill prey which they do not ingest (Gadomski and Hall-Griswold 1992) and because gorging when prey are abundant may result in rapid "pumping" of undigested salmon through the alimentary tract (Thompson 1959). Large estimates of predation losses are consistent with previously unexplained mortality of juveniles during downstream migration (Rieman et al. 1991).

Key Issue: Intra-specific and Inter-specific Compensation Could Negate the Benefits of Reductions in Predation Mortality

A multiyear evaluation was conducted on the biological response of predator populations to northern pikeminnow removals during 1990-1996. The investigators found no evidence that surviving northern pikeminnow populations compensated for sustained removals (Ward 1997):

- 1) Management fisheries in the Columbia and Snake Rivers are effective at removing large northern pikeminnow.
- 2) No evidence was found that surviving northern pikeminnow compensated for sustained removals.
- 3) No evidence was found of smallmouth bass or walleye response to sustained removals of northern pikeminnow.
- 4) No evidence was found that the diets of northern pikeminnow, smallmouth bass, or walleye changed in response to sustained removals of northern pikeminnow.

Beamesderfer et al. (1996) argued that dietary changes among other predator species following removal of northern pikeminnow are possible given enough time, but unlikely due to relatively low ($<20\%$) exploitation rates on northern pikeminnow. Beamesderfer et al. (1996) recommended evaluating the predator removal program on an annual basis and determining what is required based on the statistical power needed to detect effects of the program.

Key Issue: The Results of the Predator Removal Program Cannot Be Directly Measured in Terms of Changes in Adult Returns

Beamesderfer et al. (1996) proposed a way to indirectly measure the biological efficacy of the program. Because of the difficulties of directly measuring benefits of northern pikeminnow removal, evaluations have been based on examination of hypotheses underlying the basic thesis that low exploitation of northern pikeminnow can have disproportionately large benefits for salmon. Underlying hypotheses include:

- 1) Number of returning adults is a function of survival of juvenile salmon and steelhead during migration in fresh water.
- 2) Northern pikeminnow in mainstem Columbia and Snake River reservoirs consume significant numbers of juvenile salmon and steelhead which would otherwise have survived migration.
- 3) Large, old northern pikeminnow are the most important predators of salmonids.
- 4) The cumulative effect of a 10-20% annual exploitation rate reduces predation rate from northern pikeminnow by 50% by reducing the population of older predaceous individuals.
- 5) Target exploitation rates can be achieved and sustained with a combination of removal methods.
- 6) Northern pikeminnow population dynamics or compositions of the resident fish community do not compensate for removals.

Beamesderfer et al. (1996) reviewed evidence for each hypothesis underlying the northern pikeminnow removal program and discussed prospects for achieving and demonstrating success. Removals have little benefit during that same year because most salmonids pass before it is possible to catch significant numbers of predators (Beamesderfer et al. 1990). Instead, removal of a given fraction of the pikeminnow population reduces predation mortality in the following year. In general, an exploitation rate of 10% will reduce predation in the following year by 10% (their Fig. 6). Equilibrium is reached in 10-15 years (corresponding to the difference between the age of recruitment to the removal program and the longevity of northern pikeminnow). Exploitation rates less than 10-20% also have significant effects. For instance, 5% exploitation will reduce predation by 15-30% at population equilibrium (their Fig. 5). Greater exploitation rates produce a more rapid response (their Fig. 6). For instance, a 20% exploitation rate will reduce predation by 50% relative to the original level within 5 years and by 7% at equilibrium.

AVIAN PREDATOR POPULATIONS

In the Columbia River Basin, piscivorous birds congregate near hydroelectric dams and in the estuary around man-made islands and structures and eat large numbers of migrating juvenile salmonids (Ruggerone 1986, Roby et al. 1998). Diet analyses indicate that juvenile salmonids are a major food source for avian predators in the Columbia River and its estuary, and that basin-wide losses to avian predators are high enough that they constitute a substantial proportion of each run of salmon (Roby et al. 1998). Caspian terns (*Sterna caspia*), double-crested cormorants (*Phalacrocorax auritis*), glaucous-winged/western gull hybrids (*Larus glaucescens* x *L. occidentalis*), California gulls (*Larus californicus*), and ring-billed gulls (*Larus delawarensis*), are the principal avian predators in the basin. Populations of these birds have increased throughout the basin as a result of nesting and feeding habitats created by human activities; for example, dredge spoil deposition in the estuary (which has led to nesting islands), and reservoir impoundments and tailrace outfalls associated with hydroelectric dams (Roby et al. 1998). The breeding season for these birds coincides with the juvenile salmon outmigration which provides a ready prey source in the vicinity of the large avian colonies (Roby et al. 1998).

Caspian Tern

Caspian terns (*Sterna caspia*) are highly migratory and exhibit cosmopolitan distribution (P. Harrison 1983, C. Harrison 1984). They winter in southern California and Baja California and return north to nest (P. Harrison 1983, C. Harrison 1984). Since the early 1900s, the Caspian tern population has shifted from small colonies nesting in interior California and southern Oregon to large colonies nesting on human-created habitats along the coast (Gill and Mewaldt 1983).

The Caspian tern is the largest tern in North America, weighing about 18 oz (Harrison 1984). The terns arrive in April and nesting starts at the end of the month (Roby et al. 1998). Clutch size is usually two eggs (Harrison 1984). To avoid predators, terns construct their nests on islands (Harrison 1984), with a preference for freshly deposited sand. They are piscivorous in nature (Harrison 1984), requiring about 165 g (one-third of their body weight) of fish per day during the nesting season. Caspian terns in the west coast population are reported to live up to 27 years; over half of the fledglings reach their fourth year, and individual birds have a breeding life expectancy of nearly 9 years (Gill and Mewaldt 1983).

NMFS staff at the Point Adams Field Station (Hammond, Oregon) noted substantial increases in newly established Caspian tern and double-crested cormorant nesting colonies on man-made islands in the Columbia River estuary in the early 1990s. Because of growing concern over the increasing impacts of avian predation on salmonid smolts, NMFS requested that the Bonneville Power Administration (BPA) and the U.S. Army Corps of Engineers (COE) conduct an analysis of avian predation in the Columbia River estuary as part of the 1995 Formal Consultation on the Operation of the Federal Columbia River Power System and Juvenile Transport Program (NMFS 1995). This consultation was required to conserve several Snake River salmon species protected under the Endangered Species Act (ESA). In 1996, research was begun by Oregon State University and the

Columbia River Inter-Tribal Fish Commission and continues to evaluate the feeding habits of terns that were successfully relocated to islands closer to the mouth of the Columbia River in 1999.

Several Columbia River estuary islands on which piscivorous birds are now nesting were created by dredging the navigational channel after the Mt. St. Helens eruption in 1980. There were no terns nesting in the estuary before 1984 when about 1,000 pairs apparently moved from Willapa Bay (north of the Columbia River estuary) to nest on the newly created East Sand Island (within and near the mouth of the Columbia River estuary). Those birds moved upstream to Rice Island in 1987, and the colony has since expanded to over 10,000 pairs (the largest colony in North America).

Roby et al. (1998) reported that two colonies have become established in the Columbia River above Bonneville Dam at Three Mile Canyon and Crescent Island. These islands were created by impounding the Columbia River behind John Day and McNary Dams. Populations have fluctuated in the past at these two sites with up to 1,000 pairs in residence at each. Populations estimated from aerial photographs in 1997 were 571 pairs at Three Mile Canyon and 990 pairs at Crescent Island (Roby et al. 1998). The extent to which these populations prey on juvenile salmonids at these locations is unknown. Determining that predation level should be a priority for future study to guide appropriate management of these colonies.

Diet analyses in 1997 showed that juvenile salmonids constituted 75% of the food consumed by the Caspian terns of Rice Island (Roby et al. 1998). In the annual report for their first field season, Roby et al. (1998) estimated that the Caspian tern colony nesting on Rice Island² consumed 6.6 to 24.7 million salmonid smolts in the estuary. Final numbers are not yet available for the 1998 nesting season, but indications are that the level of tern predation in 1998 was similar to that found in 1997. Salmonid consumption rates have not been determined for Three Mile Canyon and Crescent Island.

In 1997 and 1998, between 1 and 2 million ESA-listed salmonid smolts entered the Columbia River estuary. This constituted about 1 or 2 % of the total salmonid smolt outmigration through the estuary. Roby et al. (1998) estimated that avians consumed 10 to 30 % of the total estuarine salmonid smolt population in 1997, which means that between 100,000 and 600,000 listed smolts were consumed. The large majority of salmonids consumed by Caspian terns are hatchery fish (IMST 1998); many are from hatcheries operated to mitigate the impacts of dam construction and operation on salmonids.

The NMFS, COE, U.S. Fish and Wildlife Service, BPA, and resource agencies of the states of Washington and Oregon have recently formed the Caspian Tern Working Group to develop a long-term management plan to deal with tern predation in the estuary. Early limited efforts to relocate terns farther downriver in the estuary have been successful. However, while the relocated birds exhibit an

² A description of the bioenergetics model used to develop the estimate may be found in Roby et al. (1998).

encouraging dietary shift, the true extent to which their feeding habits have changed is still unknown. Understanding the effects of relocating the rest of the Rice Island colony to downriver sites (or outside the estuary) requires further study and analysis. In addition, the impact of predation from the upriver Crescent Island and Three Mile Canyon tern colonies is unknown and requires prompt evaluation.

Double-Crested Cormorant

The most widespread of all cormorant species in North America (Sowls et al. 1980), two subspecies of double-crested cormorants (*Phalacrocorax auritis*) are found along the Pacific coast: *Phalacrocorax auritis cincinatus* (off Alaska), and *P.a. albociliatus* (from British Columbia south) (Carter et al. 1995). Both subspecies breed almost exclusively along the coast (Carter et al. 1995). Historically, there was a colony on Goat Island in the Columbia River, in Benton County, Washington (Carter et al. 1995). However, the only currently active colony in central Washington is found on Potholes Reservoir (Carter et al. 1995).

The double-crested cormorant nesting population exists on five sites in the Columbia River estuary, increasing from a few hundred birds prior to 1985 to more than 6,600 in 1992 (Carter et al. 1995). In 1997, about 6,400 nesting pairs were divided between colonies on East Sand and Rice Islands, making them the largest colonies on the Pacific coast (Roby et al. 1998). The 1,000 to 1,200 pairs of cormorants on Rice Island in 1997 and 1998 represented about 15 % of the cormorants reported nesting in the estuary (Roby et al. 1998). Cormorants abandoned the colony on Rice Island in 1999, possibly due to the efforts to relocate Caspian terns. It is unknown whether these birds relocated to East Sand Island or left the estuary.

Cormorants face into the wind when landing or taking off (Ainley 1984), and their short wings and heavy bodies require a clear runway for takeoff (Duffy 1995). Thus, colonies and roost sites are usually on unprotected portions of islands and rocks (Ainley 1984). Duffy (1995) (citing Pennycuik (1989) and Ainley (1977)) indicated that cormorant wing shape necessitates foraging efficiency - which is maximized only at short distances from colonies - and this restricts colonies to areas with reliable food sources. Garland (1998) stated that cormorants in Vermont foraged close to their nesting sites, usually within 1.4 miles.

Cormorant clutch size is four or more eggs (Ainley 1984), a large number compared to other seabirds (Duffy 1995). Incubation lasts for 25-30 days (Ainley 1984). Cormorants also exhibit asynchronous hatching, which improves hatchling survival (Duffy 1995).

The high energy demands associated with flying and swimming create a need for voracious predation on live prey (Ainley 1984). Cormorants are underwater pursuit swimmers (Harrison 1983) that typically feed on mid-water schooling fish (Ainley 1984), but they are known to be highly opportunistic feeders (Duffy 1995, Blackwell et al. 1997, Derby and Lovvorn 1997). Double-crested cormorants are known to fish cooperatively in shallow water areas, herding fish before them (Ainley 1984). Krohn et al. (1995) indicated that cormorants can reduce fish populations in forage areas, thus

possibly affecting adult fish returns. Because their plumage becomes wet when diving, cormorants spend considerable time drying out their feathers (Harrison 1983) on pilings and other structures near feeding grounds (Harrison 1984).

Double-crested cormorants usually arrive on Rice Island and initiate courtship behavior in the first two weeks of April. The average weight for adult double-crested cormorants is 2 kg and they require 500 g (or about one-fourth of their body weight) in fish per day during the nesting season. Roby et al. (1998) reported that in 1997 cormorants fledged an average of 1.61 chicks on East Sand Island and 2.11 chicks on channel markers in the estuary.

Bayer (1989) indicated that cormorants off the Oregon coast consume, on average, 0.6 to 0.8 lb daily (15 to 16% of their body weight); this is equivalent to approximately four steelhead or eight coho salmon smolts. Roby et al. (1998) estimated that cormorants in the estuary consumed from 2.6 to 5.4 million smolts in 1997, roughly 24% of their diet. As with Caspian terns, the majority of juvenile salmonids consumed are hatchery fish (which comprise more than 80% of the juvenile salmonids in the system). Many of these hatcheries also raise and release ESA-listed fish in attempts to preserve remnant wild populations.

Gulls

Ring-billed and California gull populations are increasing in the Columbia River Basin (Roby et al. 1998, York et al. in press). York et al. stated that gulls (ring-billed and California) occupy 17 islands from Chief Joseph Dam downstream to The Dalles Dam. Roby et al. (1998) estimated that over 70,000 ring-billed and California gulls are in the Richland, Washington area. Little Memaloose Island and Miller Rocks, two islands that were created by the impoundment behind The Dalles Dam, support 1,500-2,000 pairs of California and ring-billed gulls (Roby et al. 1998). Three Mile Canyon Island, created by the impoundment behind John Day Dam, supports a large colony of gulls (Roby et al. 1998). There are also colonies near the confluence of the Snake and Columbia Rivers (Roby et al. 1998), including those found in the McNary National Wildlife Refuge (Sherer 1997). Cabin Island near Priest Rapids Dam has a breeding population of 7,000 ring-billed gulls and 200 California gulls (York et al. in press).

Glaucous-Winged/Western Gull Hybrid

Off the coasts of Oregon and Washington, the glaucous-winged gull (*L. glaucescens*) and the western gull (*L. occidentalis*) tend to hybridize (Drury 1984). Substantial numbers of these hybrid gulls nest on both natural and man-made islands in the estuary. Although these gulls are not as effective as terns and cormorants at preying on juvenile salmonids - and are even more cosmopolitan in diet - they obtain much of their food by kleptoparasitism (i.e., stealing fish from terns), thereby increasing the terns' fishing needs. Salmonids constituted approximately 11% of the gulls' diet in terms of mass number in 1997 (Roby et al. 1998). The majority of salmonids taken by these gulls were hatchery fish.

California Gull

The California gull (*Larus californicus*) is one of the most widely distributed and most abundant gulls breeding in Oregon (Gabrielson and Jewett 1970). California gulls need islands with a nearby food source for nesting purposes (CDFG 1999). Nest construction and egg laying occurs in April and May, and hatching starts in June (Gabrielson and Jewett 1970, Roby et al. 1998). Two to three eggs are laid per nest (Gabrielson and Jewett, 1970), and incubation lasts for 23 to 27 days (CDFG 1999). California gulls are omnivorous (Gabrielson and Jewett 1970).

These gulls are the primary avian predators at Bonneville, John Day, The Dalles (Jones et al. 1997, 1998) and Priest Rapids Dams (York et al. in press) and, to a lesser extent, at Wanapum Dam (Ruggerone 1986). Hydroelectric dams act as bottlenecks for juvenile salmonid migration and can injure and disorient smolts, increasing their vulnerability to avian predators (ODFW 1998). There has been a major attempt to reduce predation by gulls at these dams. Avian deterrent lines, hydrocannons, and hazing have all been successful in reducing gull predation in the areas where they are employed (Jones et al. 1997, 1998). However, California gulls still take tens of thousands of smolts at mainstem dams (Jones et al. 1998).

Ring-Billed Gull

Ring-billed gulls (*Larus delawarensis*) may be found anywhere in Oregon, particularly on inland waters (Gabrielson and Jewett 1970, Drury 1984). They nest on the ground and prefer island sites (Gabrielson and Jewett 1970, Garland 1998, Canadian Wildlife Service 1999), but will nest just about anywhere, on any substrate, as long as water and food are nearby (Canadian Wildlife Service 1999). They are often found nesting with Caspian terns and herring gulls, and occasionally with California gulls and double-crested cormorants (Canadian Wildlife Service 1999). They lay two to three eggs per clutch in late April to early May; hatching occurs in June (Gabrielson and Jewett 1970, Canadian Wildlife Service 1999). Reproductive success rate is typically high (two chicks to flying age); this has led to their being the most abundant gull in North America (Canadian Wildlife Service 1999).

Ring-billed gulls are opportunistic feeders; they eat a wide variety of insects, small fish, and crayfish (Gabrielson and Jewett 1970, Canadian Wildlife Service 1999). Ruggerone (1986) found that ring-billed gulls feed extensively below Wanapum Dam on the Columbia River during the onset of the juvenile salmonid emigration in spring. This corresponds with the start of their nesting season on islands in the Columbia River (York et al. in press). York et al. found that peak salmonid consumption by ring-billed gulls occurred in May at Priest Rapids Dam. Ruggerone (1986) indicated that gulls consumed 2% of the juveniles passing Wanapum Dam.

Critical Uncertainties

In summary, avians in the Columbia River Basin kill and eat substantial numbers of juvenile salmonids every year; and may be one of the factors that limit salmonid stock recovery (Roby et al.

1998). Anthropogenic changes in the Columbia River Basin have caused increases in populations of colonial waterbirds (Roby et al. 1998). Impoundments created by mainstem dams have created islands that are ideal for gull and tern colonization. Avian predation on juvenile salmonids is being reduced by taking increasingly effective actions. Man-made islands and structures in the estuary support one of the world's largest colonies of Caspian terns as well as a large colony of double-crested cormorants. This results in the death of an estimated 10 to 30 million salmonid smolts annually. Transporting (trucking and barging) juveniles may also have an effect on predation by depositing young salmon in the estuary before they are fully smolted (ODFW 1998, Roby et al. 1998). Early arrival may delay their entry into saltwater, thus making them vulnerable to terns in the estuary (Roby et al. 1998). In addition, the physiological condition of migrating juvenile salmonids may be altered by dam passage or transportation, increasing their vulnerability to avian predators (IMST 1998, ODFW 1998, Roby et al. 1998). If losses to avian predation are to be reduced, a concerted effort must be made to alter habitat that is conducive to nesting. Moreover, bird control must be implemented at all dams in the system, and hatchery techniques must be analyzed and improved to decrease susceptibility to avian predation.

There are numerous critical uncertainties regarding the impacts of avian predation on Columbia River salmonids. In addition to broad uncertainties associated with determining the extent to which some examples of avian predation can be directly linked to hydropower effects, and the relative effects of avian predators on different salmonid populations or species, the many more specific uncertainties include: the extent of estuarine juvenile mortality resulting from the cormorant colony on East Sand Island; the extent of juvenile mortality resulting from cormorants that are residing year round in upriver locations along the Columbia River; the extent of juvenile mortality resulting from upriver gull colonies; the extent of juvenile mortality resulting from the Caspian tern colonies on Three Mile Canyon and Crescent Island; and the rate of increase or decrease in populations in these colonies.

MARINE MAMMALS

When considering all causes of salmonid decline, predation by marine mammals, while not a dominant regional cause, can be a significant local factor, especially when salmonid runs are low (NRC 1996). Marine mammals prey on salmonids near man-made structures such as dams or fish passage facilities where fish congregate and the presence of marine mammals in the Columbia River estuary during the salmonid migrations raises concern for predation on already depressed populations. A recent report to Congress identified the clear need for further study on the impacts of pinniped predation on specific salmonid runs along the west coast (U.S. Dept. of Commerce 1999). Several studies are currently attempting to quantify the consumption of adult and juvenile salmonids by pinnipeds in the Columbia River. However, it is well recognized that prey analyses based on scats (feces) are often limited to descriptive measures of dietary importance (e.g., frequency of occurrence or percentage of total prey consumed) that may be of limited use by managers (Laake et al. in prep). Estimates of the percentage of spawner escapement consumed are far more difficult to obtain and are not yet published for the Columbia River Basin. The following sections provide a summary of the status and diet of pinniped populations in the Columbia River.

Distribution of Predator Species

Three species of pinnipeds, harbor seals (*Phoca vitulina*), California sea lions (*Zalophus californianus*), and Steller sea lions (*Eumatopias jubatus*) occur in the Columbia River. Harbor seals are the most abundant pinniped species in the lower Columbia River, with peak haul-out counts exceeding 2,000 at Desdemona Sands, a tidal sandbar adjacent to Astoria which is the largest seal haul out (Laake et al. in prep.). The harbor seals require haul-out regions (e.g., mud/sand tidal flats) for resting and reproductive activities. Counts at haul-outs vary because of changes in the proportion ashore and seasonal changes in the actual numbers in the river. The number of seals associated with this haul-out region varies seasonally with the peak numbers occurring during mid-winter (Beach et al. 1985, Brown 1988). Recent seasonal averages of harbor seals for this region are: 1,659 in spring; 1,349 in summer; and 980 in fall (Laake et al. in prep.). Approximately 100-200 California sea lions utilize the East Mooring Basin at Astoria as a haul out during fall, winter, and spring (Riemer and Brown 1997). These sea lions are known to feed on discarded fish from local commercial fish processing plants in the region, making it impossible to distinguish consumption of processed fish carcasses from predation on live salmon in the river. Steller sea lions are uncommon in the Columbia River and only haul out on the South Jetty (Browne et al. in prep.).

Pinnipeds

Prey identification of pinnipeds is typically determined from analyses of fish bones, otoliths, and cartilaginous parts recovered from scats. Identification of a prey item to species depends on the type of bone recovered, the state of digestion, the amount of bone erosion, and the group of fish identified (Riemer and Brown 1997). Salmonid bone is difficult to identify to species and genetic analyses at the Northwest Fisheries Science Center promise to improve species identification of salmonid bone in scat samples. In addition, the many sources of sampling variability in the field and uncertainty with the identification of the salmonid fraction in scats, make it difficult to estimate prey consumption of pinnipeds from scat analyses. For example, among the factors that contribute to a low recovery of otoliths in scat samples is the potential for harbor seals to consume only part of a large fish. These sources of error were recently discussed and summarized at a workshop entitled "Review of Field and Analytical Methodologies for Assessing Pinniped Predation on Salmonids" held in Newport Oregon, 20-22 April 1999 (NMFS et al. 1999).

Markings (including apparent tooth and claw abrasions) commonly observed on returning adult salmon may also be indicative of marine mammal predation. Harmon et al. (1994) estimated annual injury rates of 14 to 19.2% for spring and summer chinook salmon and 5.4 to 14.2% for steelhead that arrived at Lower Granite Dam from 1990 to 1993. For the years 1994 through 1999, the injury rate for adult spring and summer chinook salmon at Lower Granite Dam ranged from 15.7 to 28.6% (Jerrel Harmon, Douglas Marsh, NMFS, pers. commun.). Based on the size of some of the teeth marks, it is believed they were made by harbor seals. A NMFS Report to Congress (NMFS 1999) under the

Marine Mammals Protection Act concluded that pinniped populations are now abundant, increasing, and widely distributed along the West Coast where there is a high potential for impacts on salmonid populations.

Harbor Seal

The diet of harbor seals (*Phoca vitulina*) is diverse with high seasonal and interannual variability, likely reflecting the availability of different prey species. When reported as percent frequency of occurrence in scat samples, the most frequently occurring prey item identified in spring (February-March) scat collections of harbor seals at Desdemona Sands in 1992-1993 was eulachon (84.3%), followed by Pacific lamprey (19.6%) and starry flounder (11.8%) (Riemer and Brown 1997). In April 1995, the main prey items identified by Riemer and Brown (1997) in scat samples were Pacific staghorn sculpin (49.3%), starry flounder (35.8%), Pacific herring (28.4%), and salmonids (19.4%). From 1995-1997, adult and juvenile salmon accounted for 6 and 19% (as percent frequency of occurrence in scats) of the diet of harbor seals, respectively (Browne et al. in prep.). During the fall, northern anchovy is the main prey item, followed by Pacific herring, salmonids, smelt species, and Pacific staghorn sculpin (Riemer and Brown 1997). Adult chinook and other salmonids appear to be much less important in the diet of harbor seals if the ranking is based on the number consumed; however, results of a biomass-based prey consumption model indicate that relatively infrequent, large prey (such as chinook) become very important in the diet when expressed in terms of percent biomass consumed (Laake et al. in prep.).

California Sea Lion

Given that California sea lions (*Zalophus californianus*) are known to feed on fish-frames from fish processing plants near Astoria, Oregon, it is difficult to determine the source or origin of their prey. Dover sole is commonly identified in the scat samples from sea lions at East Mooring Basin. Salmonid remains were identified in 19.1% of scat samples, of which 17.2% contained adult salmonid remains and 3.6% contained smolt or small salmonid remains (Riemer and Brown 1997). The National Marine Mammal Laboratory (NMFS) plans to expand scat collections in the lower Columbia River to include California sea lions that haul-out near Astoria.

At Willamette Falls, 4-10 sea lions have consumed about 200-300 salmonids (roughly 50% spring chinook and 50% steelhead, mostly winter stock) from late March through mid-May each year since 1996 (Robin Brown, ODFW, pers. commun., and ODFW unpublished data). In 1999, there appeared to be 10 different sea lions at Willamette Falls. A report summarizing observations for the past four years of pinniped predation on salmonids at Willamette Falls is in progress. Estimates of consumption will be compared with fish stock size and passage numbers of salmonids at the falls.

Steller Sea Lion

The impact of Steller sea lions (*Eumatopias jubatus*) on salmon in the Columbia River is assumed to be small (Browne et al. in prep.).

Effects of the FCRPS

Artificial structures, such as fish ladders at dams and hatcheries which channel fish through narrow areas, can slow fish passage through rivers and tributaries and effectively alter the foraging behavior of pinnipeds by generating mechanisms that concentrate their prey. Pinnipeds can take advantage of these unnatural foraging conditions, such as those that may occur at Willamette Falls where California sea lions consume salmon (Robin Brown, ODFW, pers. commun.).

Activities which remove woody debris from estuaries or rivers may also allow for more effective predation on salmonids by removing refuges required by fish to elude predators (Riemer and Brown 1997).

Alteration of River Circulation, Hydrography, and Turbidity

Operations of the FCRPS which alter the natural temporal and spatial characteristics of the flow, circulation, clarity, or turbidity of the Columbia River can alter the structure and functions of the river's ecosystem. For top trophic levels, such as pinnipeds, an alteration of the physical circulation and tidal dynamics in the river system may affect foraging ecology by changing the natural hydrodynamic features and processes that affect the availability, distribution, timing, and aggregation of pinniped prey species. There has been little research, however, devoted to these impacts. Studies of pinniped foraging have tended to focus on land-based collection of scats for enumeration of prey items. Factors in the river, such as linkages between circulation, tidal dynamics, hydrography, and prey distributions, which affect the timing and location of pinniped foraging, remain largely unstudied. It is also unknown how changes in the circulation and physical structure of the river may have changed the amount of predation occurring in the river versus the coastal marine system. Innovative, interdisciplinary research that combines studies of both the physical and biological systems will be required to fully interpret the role of pinniped foraging in the Columbia River ecosystem.

It is also unknown how activities of the FCRPS may have altered historical pinniped habitat, such as the location, areal extent, and access of suitable haul-out habitat (e.g., mud/sand tidal flats) in the Columbia River. Pinnipeds rely on sandy or rocky tidal haul-outs in estuarine or coastal habitats to rest, mate, and care for pups. The natural shifts in riverine or coastal sediments enable pinnipeds to find suitable haul-outs. This flexibility, however, can be lost due to human-encroachment on coastal habitats, dredging, or damming of rivers.

Critical Uncertainties

The present precision of estimates of the percentage of salmonid spawner escapement consumed by harbor seals in the Columbia River is poor. This is due in part to high temporal variability (interannual, seasonal, weekly, and day versus night foraging) and spatial variability in salmonid consumption and the difficulties in sampling scats sufficiently to capture all sources of variability. In addition, there is large uncertainty resulting from partitioning the scat samples containing salmonid bone that could not be identified to species. Surface observations of pinniped predation on salmonids in areas

where such observations are practical can provide a direct measure of impacts; however, an area as large as the Columbia River is difficult to monitor and can only be regionally subsampled. To extrapolate from results of scat analyses to estimates of predation also requires assessment of the pinniped population size as well as the proportion of the population that forages in a given region. For example, harbor seals in the Columbia River can forage many kilometers away from haul-out sites, including coastal regions outside of the river (Harriet Huber, National Marine Mammal Laboratory/NOAA, pers. commun., 1999). In summary, it is premature to base management decisions on the current knowledge of salmon consumption estimates for pinnipeds in the Columbia River. Additional research will be required to improve estimates.

River systems vary in the incidence of pinniped predation on salmonids and it is therefore important to define the hydrographic, ecological, and anthropogenic factors that contribute to an increased risk of predation in some rivers (NMFS et al.1999). The mechanisms and factors that influence successful foraging behavior, or threshold foraging response, of pinnipeds in northwest rivers are unknown.

The April 1999 Workshop (NMFS et al.1999) has identified the need for additional studies to “determine the factors that contribute to an increased risk of predation on salmon in some systems” and to “compare prey availability/presence in aquatic ecosystems with concurrent abundance, movements, co-occurrence, and foraging behavior of pinnipeds.” Models of risk assessment will require information that defines under what climatic, hydrographic, local meteorologic, ecological, and man-made conditions pinniped predation on salmonids becomes optimal or ineffective.

SUMMARY

Piscine Predator Populations

Dams and reservoirs of the Columbia River Basin are generally believed to have increased the incidence of predation on salmonids over historic levels. Impoundments increase availability of microhabitats within the range preferred by some predators, may increase water temperature which increases digestion and consumption rates of some predators, decrease turbidity which may increase capture efficiency of predators, favor introduced or non-indigenous competitors which may cause some predators to shift to a diet composed largely of juvenile salmonids, and may increase stress and subclinical disease of juvenile salmonids which could increase susceptibility to predation. In addition, passage conditions at dams and reduced river discharge can affect the availability, distribution, timing, and aggregation of migrating salmonids, thereby increasing exposure time to predation and, in particular, increasing exposure time later in the season when predator consumption rates are high

The primary resident fish predators in the reaches of the Columbia River Basin inhabited by anadromous salmonids are: northern pikeminnow (formerly known as northern squawfish), smallmouth bass, and walleye. Other predatory resident fishes include channel catfish, Pacific lamprey, yellow perch, largemouth bass, northern pike, and bull trout.

The northern pikeminnow, a native cyprinid, is the dominant predator of juvenile salmonids in the Columbia River system, especially in the lower Columbia River below the confluence of the Snake River to the estuary (upstream of saltwater influence). Smallmouth bass is the dominant predator in reservoirs of the lower Snake River and is co-dominant with northern pikeminnow and percids in certain reaches of the Snake system. Walleye are extremely piscivorous and are most abundant in dam tailraces where the potential for impacts on juvenile salmonids is high. A diverse and abundant community of predatory marine fishes inhabits the Columbia River estuary (within saltwater influence) and nearshore ocean used by salmonid smolts for rearing areas.

Avian Predator Populations

In the Columbia River Basin, piscivorous birds congregate near hydroelectric dams and in the estuary around man-made islands and structures and eat large numbers of migrating juvenile salmonids. Diet analyses indicate that juvenile salmonids are a major food source for avian predators in the Columbia River and its estuary, and that basin-wide losses to avian predators constitute a substantial proportion of the juvenile salmonid outmigration.

Caspian terns, double-crested cormorants, glaucous-winged/western gull hybrids, California gulls, and ring-billed gulls are the principal avian predators in the basin. Populations of these birds have increased throughout the basin as a result of nesting and feeding habitats created by human activities; for example, dredge spoil deposition in the estuary (which has led to nesting islands), and reservoir impoundments and tailrace outfalls associated with hydroelectric dams. The breeding season for these birds coincides with the juvenile salmon outmigration which provides a ready prey source in the vicinity of the large avian colonies.

Marine Predator Populations

When considering all causes of salmonid decline, predation by marine mammals, while not a dominant regional cause, can be a significant local factor, particularly when salmon runs are low. Marine mammals prey on salmonids near man-made structures such as dams or fish passage facilities where fish congregate, and the presence of marine mammals in the lower Columbia River and its estuary during salmonid migrations raises concern for predation on already depressed populations. However, the current precision of estimates of the percentage of salmonid spawner escapement consumed by marine mammals in the Columbia River is poor. This is due in part to high temporal variability (interannual, seasonal, weekly, and day versus night foraging) and spatial variability in salmonid consumption, and the difficulties in sampling sufficiently to capture all major sources of variability.

Three species of pinnipeds, harbor seals, California sea lions, and Steller sea lions, occur in the Columbia River. Harbor seals are the most abundant pinniped species in the lower Columbia River, with peak haul-out counts exceeding 2,000 at Desdemona Sands, a tidal sandbar adjacent to Astoria,

Oregon, which is the largest seal haul out. However, harbor seals in the Columbia River can forage many kilometers away from haul-outs, including upriver areas and coastal regions outside the river.

In general, very little is known regarding how the existence and operation of the FCRPS may have altered the historical habitat and salmonid consumption rates of marine mammals.

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